The interplay of habitat and seed size on the shift in species composition in a fragmented Afromontane forest landscape: Implications for the management of forest restoration

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A thesis submitted in fulfilment of the requirements for a PhD in Ecology at the University of Canterbury.

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2014

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ACKNOWLEDGEMENTS

Thanks so much to my supervisor, Associate Prof. Hazel Chapman, for being highly knowledgeable, approachable, motivating and supportive. Prof. P. M. Forget thanks for giving me the audience to discuss my ideas with you. It was a great privilege for me to work with those among the world's best in this field. You were both perfect supervisors.

Thanks to Prof. Mahdi, the Vice Chancellor Gombe State University and Associate Prof. Hazel Chapman, the Director of the Nigerian Montane Forest Project for this wonderful opportunity. Dr. Elena Moltchnova Statistical Consultant thanks for your advice and guidance on statistical analysis.

Gombe State University and Nigerian Montane Forest Project awarded me funding scholarships which were greatly appreciated.

For assistance in the field I thank Hammadu Adamu, Misa Zubairu, Yakubu, Hamma Sumo, Thomas, Bappa Manu, Hammadu, and all other field assistants whose names were not mentioned. You were all integral parts of this work in many ways.

Matt Walters thanks for your guidance on the photographs and figures used in this study. I greatly appreciate all the help, support and encouragements from Dr. Mohammed Musa.

I really appreciate all helpful advice from Alexander Knight, Isyaka Tom, Dr. Shelley Chappell, Charles Nsor,Denise A. Lambaer, Paul Dottun, Andrew Barnes, Abby Grassham, Ossy one, Sasha and Kelly Hutchinson. A special thank you to Josh Thia for taking his time to share ideas and helpful advice during this study.

Big thanks to my wife, children and parents for the tolerance and patience for leaving them in Nigeria during the period of this study in New Zealand.

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ABSTRACT

The Cameroon Highlands that run along the Cameroon-Nigeria border are an important source of biodiversity. Not only are they rich in species and high in endemics, but biota from West Africa have not been studied as extensively relative to other parts of the Afrotropics, or the tropics in general. Threatening these rare and diverse habitats is anthropogenic pressure, which fragments forests and changes local animal communities. This thesis wished to address the impact of humans on seed dispersal and recruitment processes on selected tree species in forests on the Mambilla Plateau—a montane region in Nigeria's north-east. Research was conducted at Ngel Nyaki Forest Reserve, a conservation area established by the Nigerian Montane Forest Project. The reserve comprises a moderately-large forest patch (Ngel Nyaki Forest) and many small riparian fragments embedded in a grassland matrix. Cattle grazing and burning of this grassland are major threats to the survival of forest in this area.Hunting of local wildlife for bushmeat is also of concern, considering many of the region's large-mammalian fauna are now locally extirpated (e.g. elephants) or at low abundances (many primate species). Loss of large-bodied frugivorous species has the potential to negatively impact the recruitment of large-seeded tree species that solely rely on them as seed dispersers. In this study, the ability for scatterhoarding rodents to act as surrogate dispersers for large-seeded species is tested. While much research has been carried out on secondary rodent dispersal in the Neotropics, work in the Afrotropics is still in its infancy. Because the outcome of plant-rodent interactions (i.e. predated or dispersed) may vary with season, habitat, or traits of the seed species in question, a number of experiments were established to quantify how local rodents at Ngel Nyaki may or may not be acting as effective dispersers. Additionally, the benefits of rodent dispersal were examined by creating an experiment that simulated secondary dispersal on seedling recruitment. The results of this study demonstrated that rodents can act as effective dispersers in Afromontane forests, but this is influenced by habitat, seasonal abundance of resources, and palatability of seed species. Furthermore, it was demonstrated that burial of seeds by rodents can increase the establishment probability of a seed by protecting it from removal by other rodents. However, while rodents play a strong driver of seed survival, it was also demonstrated that seedling mortality factors (such as herbivory) can also be heavy filters to seedling success. It is hoped that the results of this study will help to inform better management decisions and understand how the composition of the forest might change in the future.

CHAPTER 1

Seed dispersal, tropical forest regeneration, and the impacts of human disturbance: A review

1.1 INTRODUCTION

1.1.1 Seed dispersal

Trees are sessile organisms and any major dispersal events are associated with reproduction (Dick *et al.* 2008; Bacles & Jump 2011). Seed dispersal involves moving seeds away from the parent plant, a vital process that links reproduction and further growth and establishment (Harcombe 1987; Schupp *et al.* 1989). Seed dispersal may occur by abiotic factors such as gravity, wind, water and/or ballistic release of seeds(Roberts & Haynes 1983) or by animal-mediated movement (Levey *et al.* 2002; Forget & Jansen 2005). Seed dispersal is vital for preserving species from extinction and maintaining their diversity (Janzen, 1970; Connell, 1971; Forget & Milleron, 1991; Guariguata & Pinard, 1998). The establishment of tropical tree communities is directly impacted by seed dispersal, which in turn, varies with the dispersal mechanisms of the species that inhabit such communities (Dennis et al., 2007). Seed dispersal is a significant part of the early life stages of forest plants, linking adult reproduction with growth and development (McConkey *etal*., 2012). For many species, escape from parental trees increases the likelihood they will germinate and be recruited to the next stage in the plant's life cycle (Connell 1971; Schupp *et al.* 2010). Hubbell (1980) also indicated that high seed density under the parent plant can lead to predator satiation and result in a high rate of seed dispersal.

What appears common is that seed dispersal is rarely mediated by a single dispersal agent. Diplochory, as defined by van der Pijl (1969), describes a two stage movement of seeds by different vectors (Wenny 1999; Forget *et al.* 2005; Beck & Vander Wall 2011). Each step provides different benefits to the plant: while the first step represents movement away from any potential limiting influences of the parent plant, the second step involves horizontal movement into sites that provide greater probabilities of seedling establishment (Wenny 1999; Beck & Vander Wall 2011). For example, a dispersed seed settles at its first deposition site by an initial dispersal vector such as wind, gravity or a frugivore, but is then secondarily

moved on by some other mechanism such as a scatterhoarding rodent (Herrera & Jordano 1981; Vander Wall & Joyner 1998; Zhang & Wang 2001; Bortiri *et al.* 2006). Seeds handled by these secondary rodent dispersers may not remain where they are originally placed, as they may be moved to farther subsequent deposition sites by the same or other rodents (Vander Wall & Joyner 1998; Soné & Kohno 1999; Jansen *et al.* 2012a).

1.1.2 Seed dispersal effectiveness

The effectiveness of seed dispersal has important implications for the demographic and genetic structures of plant species (Makana & Thomas 2004; Dick *et al.* 2008; Bacles & Jump 2011). Schupp (1993) defines the effectiveness of seed dispersal by animals as an empirical measure that takes into account the quantity of seeds dispersed and the quality of dispersal from the parent plant to a suitable microsite. The distance and the site to which a seed is transported from the parent plant by the disperser (i.e., the quality of dispersal) may vary depending on the plant species (Wenny 2000). However, the seed of different species may have varying palatability to dispersers/predators, for example: in the Neotropics, seeds of some Sapotaceae species are more preferred by scatterhoarding rodents than those of the family Clusaceae (Chauvet *et al*., 2004; Feer & Forget, 2002). This difference in palatability may facilitate or hinder the dispersal process of tree seeds (Howe & Smallwood 1982; Aliyu *et al.* 2014). The constraints on the effectiveness of seed dispersal may vary with fruit and/or seed morphology across plant families (Liu *et al.* 2012).

1.1.3 Seedsize

Seed size plays an important role in determining the dispersal ecology of different species' seeds. Firstly, seed size sets constraints on the range of frugivores that are capable of dispersing them; however, even though large seeds (>20 mm in diameter) comprise a limited subset of the possible disperser pool, there are positive correlations between size and the probability of successful establishment (Westoby et al., 1996; Thompson & Fenner, 2005). Seed size is thought to have evolved as a trade-off between producing many smaller seeds, each with few resources, and fewer larger seeds, each with more resources (Hastings 1980; Tilman 1994; Rees & Westoby 1997; Vujnovic *et al.* 2002). Large seed reserves are among the features of many tropical tree species (Baraloto & Forget, 2007; Foster & Janson, 1985; Metcafe, 1995), and the value of these reserves may include: (1) large seed mass, which may

tolerate seed predators' partial consumption (Bongers & Hemerik, 2004; Wang et al., 2012); (2) a greater probability of seedling establishment if these seeds are buried (Jansen et al., 2004; Vander Wall, 1990); (3) at the post-seedling establishment stage, seed reserves can be used to replace seedling tissue consumed by herbivores (Van Uytvanck et al., 2010) or damaged by trampling (Clark & Clark 1996); and (4) large seed mass may also provide a source of energy reserves that can be used to supplement photosynthetic carbon for seedlings that persist for long periods under very low light conditions (Baraloto et al., 2005).

In some species, cotyledon reserves of seeds are retained for weeks or months after the production of a functional leafy shoot (Edwards & Gadek 2002). It has been suggested that this delayed use of cotyledon reserves may in part be determined by the seedling's light environment (Everham *et al.* 1996). However, there is a compromise between two opposing selective pressures pertaining to size. On one hand, larger cotyledons can favour germination, survival and growth of seedlings particularly under canopy (Howe 1990; Souza & Válio 2001). On the other hand, the higher nutritional content in larger cotyledons, and their attractiveness to predators, can increase the probability of predation (Milberg & Lamont 1997). However, Garwood (1983) argues that irrespective of seed size and despite the capacity of large seeds to germinate in the shaded understory, many have seedlings that do not survive in shaded conditions, suggesting that they require light to become established (Fu *et al.* 2010). Where seedling establishment conditions might favour larger seeds, maximum seed size can be constrained by disperser size (Howe 1990). Thus, studies on seed dispersal, germination and seedling survival in different forest habitats are vital in order to determine the effects of fragmentationon forest community composition (Schupp 1988; Houle 1998).

1.1.4 Germination and establishment

Important factors in determining the success of germination are water availability, tolerance to desiccation, light quality and temperature (Bazzaz & Pickett 1980; Yu *et al.* 2008). Seeds of late successional species with large seeds tend to have higher water content and reserved resources in their cotyledon, which enables them to germinate under shady conditions (Bazzaz & Pickett 1980; Swaine & Whitmore 1988). Research shows that some shade-tolerant species may have smaller seeds than light-demanding species (Kelly & Purvis 1993). Some seeds may remain dormant in the seed bank until fire or treefall opens up gaps and increases light exposure (Valleriani & Tielbörger 2006). The site where seed is deposited determines whether it will germinate. If sites beneath parental trees are less suitable than

those away from them, there is benefit to germinating post-dispersal (Egawa & Tsuyuzaki 2011). In some cases, it seems that the movement of seeds to sites away from parental influences significantly increase the chances of germination compared to seeds that fall directly beneath the parent plant (Wenny 2000; Egawa & Tsuyuzaki 2011). Such a phenomenon has been explained by the Janzen-Connell Hypothesis, which postulates that sources of species-specific mortality (predators and pathogens) are at greater densities around conspecific trees, and consequently, seeds benefit from dispersal away from parental trees (Janzen 1970; Connell 1971).

Germination, however, does not guarantee seedling survival, regardless of dispersal mode (Chambers et al., 1999; Marines et al., 2013). The reasons being that, apart from edaphic and climatic conditions, other environmental factors such as seed predation post-dispersal (Brewer & Rejmánek 1999), seedling herbivory (Asquith *et al.* 1997), attack by pathogens (Augspurger 1984) and desiccation appear to be serious hindrances to seedlings establishment at recruitment sites (Jenny *et al.* 2014). Hence, understanding the relationship between the factors that retard seed dispersal and the causes of seedling mortality after seed germination is crucial.

1.1.5 Anthropogenic disturbance and the future of tropical forests

Ongoing anthropogenic activities associated with increased human population pressure have caused major disturbances and/or loss to plant and animal habitats in tropical forests (Smith *et al.* 1999; Styger *et al.* 2007). Indeed, evidence shows that habitat disturbance in the tropics is among the most immediate causes of the diminished diversity of plant and animal species seen today (Houle 1998; Kollmann 2000; Laurance *et al.* 2004; Sodhi 2007).

Forest fragmentation may have profound effects on community ecological interactions: the reduction in forest size and increased disconnect amongst forest patches leads to changes in plant and animal species abundance and diversity (Stouffer & Bierregaard 1995; Benítez-Malvido & Martínez-Ramos 2003; Cramer *et al.* 2007b), which has consequences on vertebrate-directed seed dispersal (Connell & Green 2000; Tomimatsu & Ohara 2004; Cordeiro *et al.* 2009). For example, Cordeiro and Howe (2003) demonstrated that a loss of bird species in forest fragments resulted in poor seed dispersal, and reduced seedling recruitment of an avian-dispersed rainforest tree. Fragmentation of forest habitat reduces population densities of top predators, large-bodied vertebrates, and specialists, which

is expected to have damaging effects on tropical forest ecosystems eg seed disperal (Babweteera *et al.* 2007; Kirika *et al.* 2008a). This jeopardises the future of tropical forests (Laurance *et al.* 2012; Harrison *et al.* 2013), and is especially pertinent in highly human populated localities with high levels of poverty (Burgess et al., 2007; Karanth, 2007).

The early life stages of trees (seed dispersal, germination and seedling survival) appear to be the most susceptible to disturbance (McConkey & Brockelman 2011). Disruption of seed dispersal is now recognised as one of the major threats to the future of many tropical forests because up to 70% of tropical forest tree species produce fleshy fruits that have evolved for primary dispersal by animals (Howe & Smallwood, 1982; Levey et al., 2002; McConkey et al., 2012). This primary seed dispersal is carried out by frugivorous birds (Cordeiro & Howe 2003; Weir 2004), bats (Lobova et al., 2009), primates (Chapman & Chapman, 1996; Julliot, 1996), and much larger mammals such as elephants (Cochrane 2001; Babweteera *et al.* 2007; Babweteera & Brown 2009). This high dependence of tropical tree species on vertebrate-directed seed dispersal makes them particularly vulnerable to frugivore decline and/or extinction (Babweteera *et al.* 2007; Kirika *et al.* 2008b; Babweteera & Brown 2009).

Consequently, the effect of large-vertebrate defaunation may likely depend on the fruit or seed size of the tree species (Cramer *et al.* 2007b) and the presence or absence of other dispersers (Jansen *et al.* 2012a). Furthermore, a large seed (> 20 mm in diameter) can only be dispersed by large-gaped frugivores, while small seeds (< 10 mm in diameter) are dispersed by both large and small gaped frugivores. The proportion of frugivores in a community that may disperse a particular seed taxa increase with decreasing fruit/seed size (Mack 1993; Chapman & Chapman 1996; Jordano *et al.* 2007). While a disperser needs to have a gape wide enough to swallow a seed, large fruits and seeds can be predated upon by animals of any size; this suggests that plants with large seeds (versus smaller-seeded species) may be more vulnerable to forest disturbance and consequential loss of large-bodied seed dispersers (Fragoso 1997; Githiru *et al.* 2002; Bollen *et al.* 2004; Guimaraes *et al.* 2008).

1.1.6 The impact of hunting on seed dispersal agents

The directed hunting of large-bodied animals suggests that the distribution and diversity of large-seeded species may be constrained by the decline of large frugivore dispersers (Wright *et al.* 2007). In the Neotropics many large-seeded species are reported to

have lost their presumed frugivores during the Pleistocene (Janzen 1988) and yet, survive today. Seed dispersal facilitated by rodents may be relied on by large-seeded trees in the Neotropics (Forget 1990). Large frugivorous vertebrates might be more affected by forest disturbance than scatterhoarding rodents, which may experience lower hunting pressures and are less sensitive to habitat changes than large frugivores (Wright 2003; Dirzo *et al.* 2007). Studies also indicate that secondary seed dispersal through scatterhoarding rodents may be essential for the prevalence of large-seeded fruit species after the extinction of their primary seed dispersers (Tabarelli & Peres 2002; Guimarães *et al.* 2008). A significant determinant of seed dispersal effectiveness is likely vertebrate body size, since it scales with the rate and extent of animal ranging (Peters 1983). Large-bodied seed dispersers, because they range beyond the distances covered by smaller-bodied vertebrates, should be particularly proficient at moving seeds sufficiently faraway to overcome Janzen–Connell effects (Fragoso & Huffman 2000; Guimarães *et al.* 2008), maintaining gene flow between isolated stands of trees (Chapman & Onderdonk 1998), reintroducing rare species to habitat patches where they have become locally extinct (Hovestadt *et al.* 1999), and preventing germination sites from being won by poor competitors (Hurtt & Pacala 1995; Tilman 1999).

1.1.7 Interaction between scatterhoarding rodents and fragmentation

Defaunation—with particular reference to loss of large frugivorous vertebrates—tends to have negative impacts on seedling recruitment of large-seeded species (Cardoso da Silva & Tabarelli 2000; Wright 2003; Guimarães *et al.* 2008; Holbrook & Loiselle 2009). However, compensation of seed dispersal by other sympatric animals might reduce such negative effects (Brewer & Rejmánek 1999; Wright *et al.* 2000; Wright 2003), and the role of rodents as secondary dispersers may play a pivotal role in forest regeneration (Hubbell 1980; Forget 1990; Haugaasen *et al.* 2010; Kuechly *et al.* 2011; Jansen *et al.* 2012b). Secondary seed dispersal is any horizontal movement and distribution of viable seed after the initial movement by primary dispersal vectors (Vander Wall 1990). Scatterhoarding by rodents is a behaviour evolved to stockpile resources when they are abundant for future use (Vander Wall 2010). Plants benefit from scatterhoarding, as there is the chance that seed will escape predation, survive and germinate (Vander Wall 2010; Koike *et al.* 2012). Subsequently, scatterhoarding rodents can be viewed as conditional mutualists (Theimer 2005; Vander Wall 2010).

The degree to which rodents act as mutualistic seed dispersers lies along a predation–

mutualism gradient (Theimer 2005): consumption of excess seed that limits plant population growth pushes rodents toward the antagonistic predator role, whilst adequate movement of seed and predation rates low enough to allow recruitment lend them to acting as mutualists. Scatterhoarding rodents can move large seed (>20 mm in diameter) and their movement of seeds increases the dispersal distance from parental plants, facilitating seedlings success (Janzen 1970; Connell 1971; Jansen *et al.* 2012b). Extensive research in the Neotropics has demonstrated that seed dispersal by scatterhoarding rodents can increase the chances for seedling survival since seeds are moved away from the parent plant (Forget, 1997). This is because much of the seed predation and attacks by pathogens that prevent seedlings from establishing is concentrated under adult trees (Janzen 1970; Connell 1971; Augspurger 1984; De Steven 1994).

As forests become fragmented and frugivore dispersers decline, the interplay between niche availability, seed dispersal, seed size and chance will play a large part in defining fragment diversity and composition (De Steven, 1988; Forget, 1994; Balderrama et al., 2005; Carvajal & Adler, 2008). Furthermore, the conditionality of secondary dispersal mutualisms is dependent on a number of contributing factors (i.e. food availability, seasonal variance in predator and seed abundance, and species-specific seed traits), and fragmentation may exacerbate any drivers that push rodents toward being more antagonistic (Asquith et al., 1997; Cramer et al., 2007a; Haugaasen *et al.* 2010).

In Africa, many plant species benefit from dispersal by large vertebrates—e.g. elephants, antelopes and chimpanzees—yet these animals are some of the first to disappear through intense hunting practises (Babweteera *et al.* 2007; Babweteera & Brown 2009, 2010; Fiona *et al.* 2013). Therefore, in the absence of large-bodied vertebrates, can rodents effectively disperse seeds? Firstly, burial of seeds may reduce the chances of seeds being predated or attacked by pathogens, and also prevent seed desiccation and promote the ability of seeds to germinate (Hollander & Vander Wall 2004; Roth & Vander Wall 2005; Briggs *et al.* 2009; Guo *et al.* 2009). Secondly, scatterhoarding rodents reduce chances of seedling herbivory under parent plants by dispersing seeds farther from parent plants. Finally, scatterhoarding rodents may also limit intraspecific and interspecific competition among seedlings by dispersing clumps of seeds, thus reducing inter-seedling competition (Connell, 1983; Cross & Benke, 2002; Kuhn & Beck 2005).

1.2 THIS PRESENT THESIS

1.2.1 Study site

The study was conducted within Ngel Nyaki Forest Reserve on the Mambilla Plateau, in Taraba State, Nigeria (7^{o} 5'N, 11^{o} 3'E; Figure 1.1). The reserve covers a total area of 4600ha and includes 750ha of almost continuous mid-altitude sub-montane forest at 1400−1600m elevation (Chapman & Chapman 2001). This forest is embedded within a savannah-grassland landscape of *Sporobolus* grasses (Chapman & Chapman 2001; Beck & Chapman 2008; Adanu *etal*. 2010). The mean annual rainfall is 1800mm (Nigerian Montane Forest Project, NMFP, rainfall data) and the mean monthly maximum and minimum temperatures for the wet and dry seasons are 26 and 13°C, and 23 and 16°C, respectively (Matthesius *et al.* 2011). The reserve is officially protected by the Taraba State Forest Service and the presence of NMFP researchers also has a positive influence on reducing poaching. However, local Fulani pastoralists and their cattle still remain on the reserve land, and their cows enter the forested areas, trampling and eating seedlings and compacting soil (Chapman & Chapman 2001). Additionally, the grassland is annually burnt to encourage new growth; fires encroach into the forest edge, opening it up and encouraging the growth of light demanding lianas and grasses. Outside the main Ngel Nyaki Forest, small riparian forests (Figure 1.2). The small riparian forests also presumably suffer from cattle browsing, trampling, fire encroachment,as well as the removal of poles for fence posts and fuel by the local Fulani families.

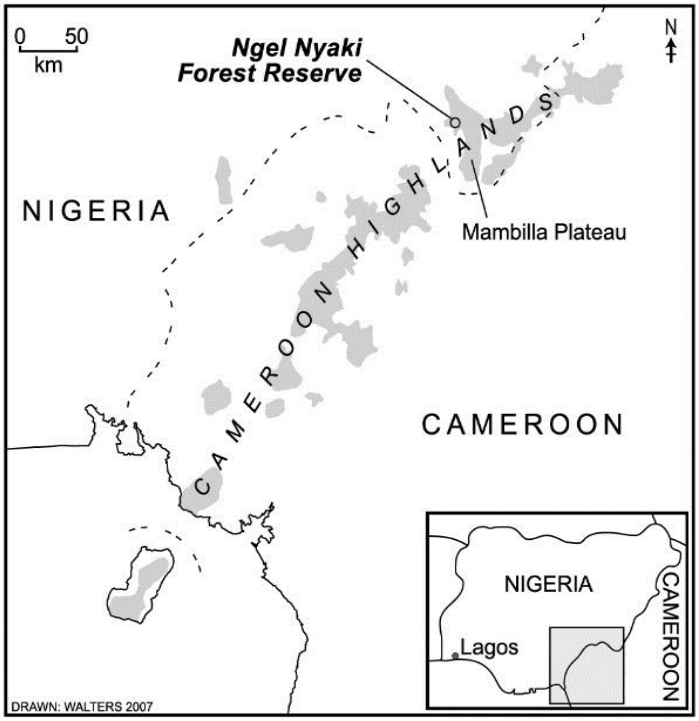

Figure 1.1: Location of Ngel Nyaki Forest Reserve on the Mambilla Plateau in the south-eastern corner of Nigeria. The Mambilla Plateau constitutes a region of the Cameroon Highlands which run along the border of Nigeria and the Cameroon. The shaded areas are forest.

Figure 1.2: Forest habitats at Ngel Nyaki Forest Reserve. The main forest (Ngel Nyaki) is a large forest patch surrounded in a matrix of grassland (left). Amidst the grassland, along the banks of small streams, are small riparian fragment forests (right).

Within this study three different habitat types are explicitly referred to. These are: the core forest (COR), which is untouched by cattle and burning; the forest edge (EDG), which is defined here as the first 200m of forest (starting at the forest/grassland border); and riparian forest fragments (FRG), which follow streams in the grassland surrounding Ngel Nyaki Forest. In terms of the level of degradation, FRG > EDG > COR: as described above, cows enter both the FRG and EDG habitats, and both are under threat from fire encroachment. In addition, FRG are dramatically smaller patches of forest, and thus of lower ecological quality. Three sites were selected per habitat—each at least 200m from each other (Figure 1.3).

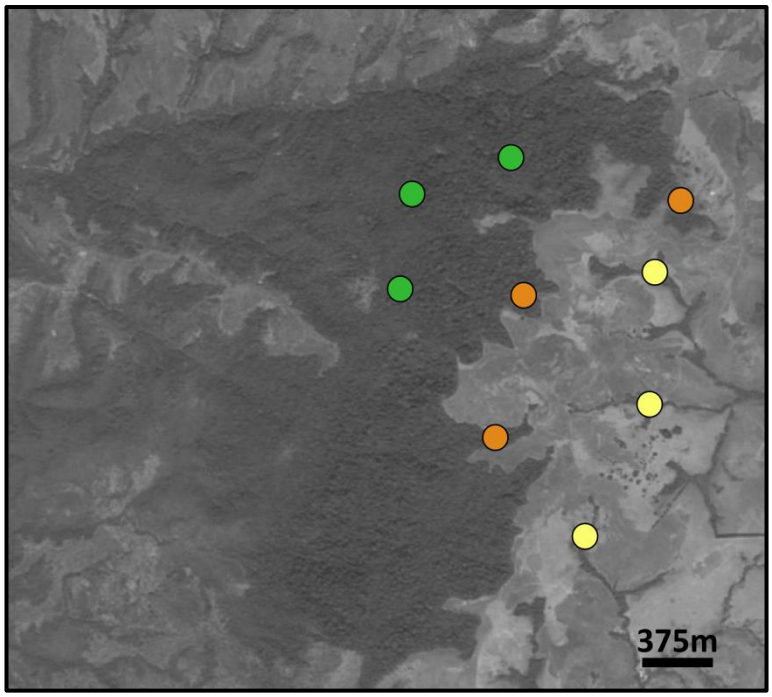

Figure 1.3: Study sites used in this thesis. Sites were spaced 200m apart from each other in the core forest (COR, green dots), in the forest edge (EDG, orange dots), and in the riparian fragments (FRG, yellow dots).

1.2.2 Research goals

The seed dispersal services of scatterhoarding rodents are a focus of this thesis, and the research presented here explores how these potential dispersal agents may assist the focal tree taxa in the degraded montane forest system where the study was conducted. In Chapter 2, the conditionality of secondary seed dispersal mutualisms are addressed: specifically, the impact of habitat and palatability of seed species on whether or not scatterhoarding rodents act only as antagonistic predators versus mutualistic dispersers. In Chapter 3, the importance of

scatterhoarding rodents as substitute dispersers for a species that has totally lost its large (supposedly elephant dispersed) vertebrate mammalian disperser is addressed; specifically dispersal by rodents of the large seeds of *C. oreophila* was investigated, and the consequence of habitat degradation on this dispersal service. In Chapter 4, a multi-factorial experiment was used to understand abiotic and biotic filters that may limit the establishment of the focal tree species in different habitat types. This has consequences for regeneration of trees and possible future community composition. Finally, in chapter five, the results are summarised and discussed in terms of their implications to managing tree species in the Ngel Nyaki forest and Afromontane habitats more generally, as well as the possible community consequences of habitat degradation.

1.2.3 Study species

Five species were selected based on their seed size (moderate to large size), requirements for dispersal and habitat for establishment:*Anthonotha noldeae*, *Carapa oreophila*, *Garcinia smeathmanii*, *Pouteria altissima*, and *Syzygium guineense* (Table 1.1).

Anthonothanoldae (Figure 1.5a) Rossberg (Fabaceae) is among the larger tree species with large seeds (> 20 mm) in Ngel Nyaki. Fruiting phenology varies with age, although a few trees fruit annually. The most common fruiting months are March through May (Nigerian Montane Forest Project (NMFP) phenology data). This species is commonly found in the edge habitat and open areas of the core forest but is absent in the fragments.

Carapaoreophila (Figure 1.5b) Kenfack (Meliaceae) is an endemic tree to Cameroon and the eastern Nigerian highlands (Chapman & Chapman 2001). It is distributed in montane regions at altitudes ranging from 1100–2500m above sea level. *Carapaoreophila* is common within the Ngel Nyaki forest particularly in more humid west-facing slopes and close to streams (Aliyu unpubl. data). It is less common in the riparian fragments. It is possible the large fruit has evolved to be consumed and dispersed by large mammals such as elephants (Blake *et al.* 2009), which are locally extinct.Seeds are now more likely dependant on rodents for secondary dispersal as observed among members of same genus in the Neotropics

Garcinia smeathmannii (Figure 1.5c) Oliver (Clusiaceae) is common in the three habitats. Fruiting phenology varies among years but fruiting is mostly towards the end of dry season, between November and January (NMFP phenology data 2010). Primates swallow the fruit of *G. smeathmannii* while the Cameroon olive pigeon (*Columbussjostedti* Reich) and the

piping hornbill (*Bycanistes fistulator* Cassin) feed on fruit pulp and drop seeds under the parent trees (Ihuma 2007). Bats suck *G.smeathmannii* fruits and sucked seeds can sometimes be seen accumulating on the bare ground under bat roosts (pers. comm. P.M. Forget, 2011).

Pouteriaaltissima (Figure 1.5d) A. Chev. Baehni (Sapotaceae)was included in this study due to its endangered status and decline in the fragment and the edge habitats, but it is common in the core forest habitat (Aliyu unpubl. data).

Syzygium guineense (Figure 1.5e/f) Willd (Myrtaceae) is an evergreen of medium height tree. Trees were in fruit between January-June in 2005; February-June in 2006; April-June in 2007; March, May and June in 2008; and January, April and May in 2009 in Ngel Nyaki (NMFP phenology data 2010). This species is common in the fragment but rare in the edge and forest core habitats.

Before experiments were conducted, a preliminary investigation (Aliyu, unpub. data) was carried out to determine the distributions and abundances of each focal tree species in the COR, EDG and FRG (Figure 1.4). Briefly, in each of the habitats a 100 m line transect was marked, five meters on either side of the line was marked. This was replicated five times in each habitat at about two hundred meters apart. These results demonstrated some species show habitat restrictions, and that current recruitment patterns (abundance of juveniles) is also habitat-dependent.

Focal species morphological features were used in distinguishing the categories (seedlings, saplings and adults). Seedlings were erect and unbranched shoot , saplings bared anchored shoot with less than 3 cm diameter at breast height (dbh) (1.4 m) and bear branches. Leaves of seedlings were smaller in size than those of saplings. Focal species with more than 3 cm dbh was considered a tree. The mean of fifty percent of collected data on height per species for each category (seedlings, saplings and trees) was considered as the height for each of the category.

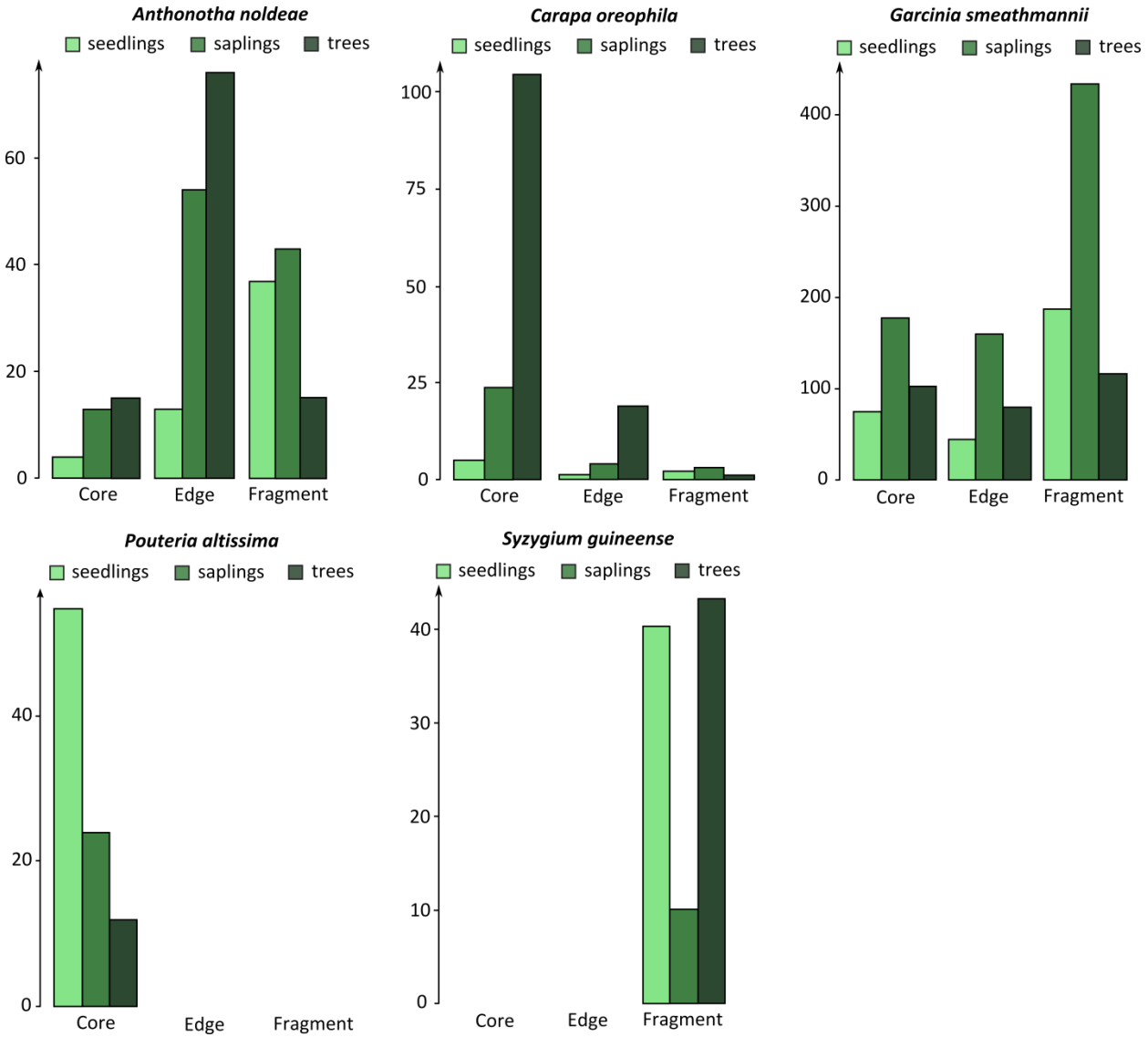

Figure1.4: The distribution and abundance of juveniles and adult trees in different habitats for focal species. Seedling, sapling and tree height varied with species, for *Garcinia smeathmannii* the height ofseedling is ≤ 20 cm, sapling ≤ 100 cm ≥ 100 cm tree. For *Carapaoreophila* seedling height is ≤ 25 cm, sapling ≤ 160 ≥ 160 cm tree. *Anthonothanoldeae* seedling ≤ 25 cm sapling ≤ 160 ≥ 160 tree; *Pouteriaaltissima*seedling ≤ 25cm sapling ≤ 400 ≥ 400 tree and *Syzygium guineense* seedling≤ 10cm sapling ≤150 ≥ 150 tree. The seedling, sapling and tree height were also estimated.

Table 1.1: The five study species, with family, tree height, fruit sizes, fruit type and colour and average (n=30) number of seeds per fruit and seed sizes. Habitat indicates which of the forest types (COR, EDG, FRG) this tree species has been observed in at Ngel Nyaki.

Species	Family	Tree height (m)	Estimated fruit size (mm)	Fruit type and colour	Seeds/fruit	Estimated seed size (mm)	Habitat
A. noldeae	Fabaceae	20(±9.2)	120(±3.5) x 40(±1.4)	Pod, hard brown	4 (± 0.5)	30(±0.9) x 25(±1.0)	COR EDG
C.oreophila	Meliaceae	12(±6.7)	130 (± 1.9) x 10 (± 0.8)	Berry, hard brown	14 (± 2.8)	30 (± 0.6) x 25 (± 0.5)	COR EDG FRG
G. smeathmannii	Clusiaceae	9(±3.6)	35 (± 0.9) x 41 (± 0.71)	Drupe, fleshy, green	2 (± 0)	28 (±0.43) x 27 (± 0.38)	COR EDG FRG
P.altissima	Sapotaceae	40(±4.1)	41 (± 0.81) x 32 (± 0.49)	Drupe, fleshy, green	1 (±0)	30 (± 0.33) x 15 (± 0.21)	COR
S.guineense	Myrtaceae	25(±7.0)	2.3(±2.0) x 1.5(±1.4)	Drupe, fleshy Purple/black	1 (± 0)	13(±0.2) x 10(±0.1)	FRG

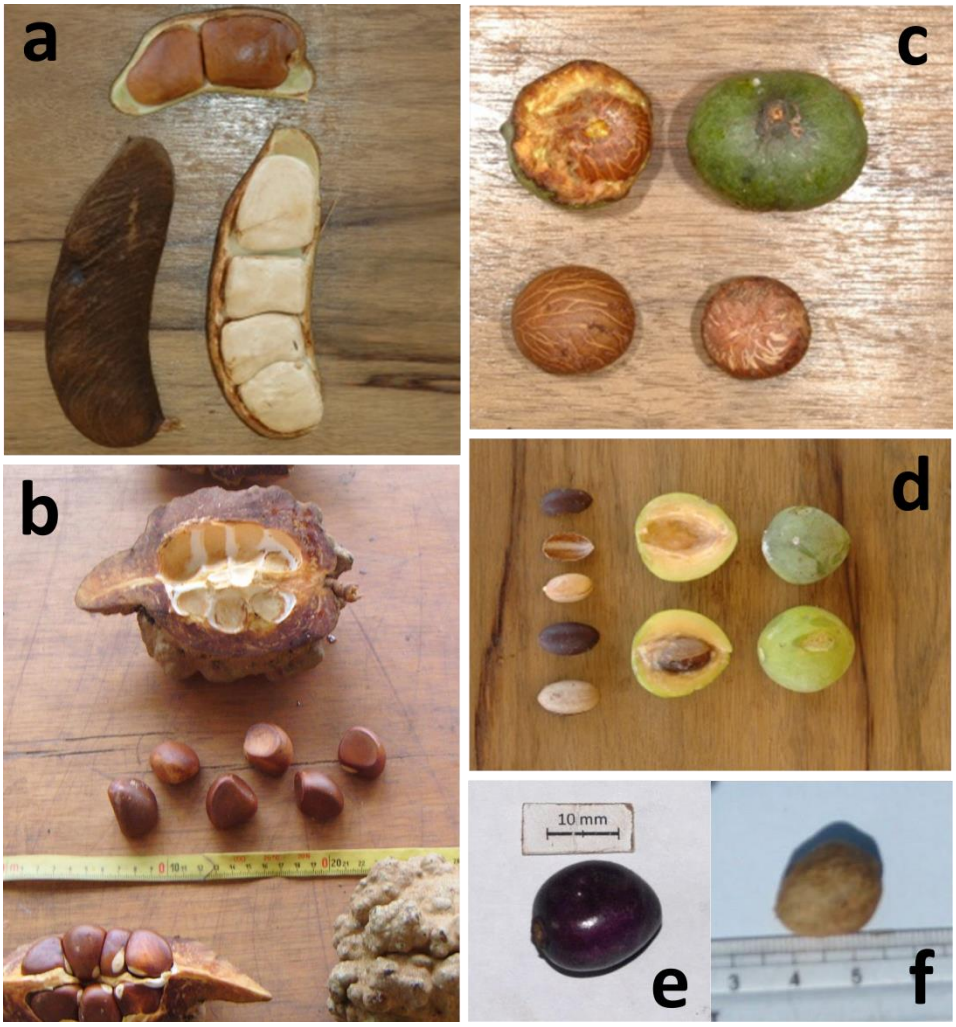

Figure 1.5: Fruit and/or seeds of the study species. (a) *Anthonothanoldeae*; (b) *Carapa oreophila* (c) *Garcinia smeathmannii* (d) *Pouteria altissima* (e/f) *Syzygium guineense.*

1.2.4 Statistical analyses

Since all of the analyses were concerned with the analysis of categorical response (for example seed fate could be categorized into predated, cached, buried and missing, I have used a mixed effects multinomial logistic regression model. I have chosen to implement it within the Bayesian framework both, because of the flexibility of the Bayesian approach, and because of the availability of the statistical software package WinBUGS (Spiegelhalter *et al*. 2002). Bayesian inference is increasingly used in ecology (Ellison 2004) and see McCarthy (2007) for an introduction to Bayesian methods in ecology.

CHAPTER 2

The interplay of habitat and seed type on seed fate in a fragmented Afromontane forest landscape

2.1 ABSTRACT

Very little is known about scatterhoarding by rodents and its potentially vital role in secondary dispersal and forest regeneration in Africa. This scholarly gap needs filling, particularly as Africa has the second highest rate of deforestation globally and deforestation rates in Nigeria, the location of this study, exceeded that of all other countries. As levels of defaunation in Africa are also high, the fate of large seeded species which are most vulnerable to the loss of primary dispersers is in question. The study site was a degraded Afromontane landscape with stands of forest in varying levels of degradation/fragmentation. Using thread marked seed I tested the hypotheses that i) the balance between seed predation and dispersal will favour predation in degraded/fragmented forest relative to continuous forest and ii) that rates of scatterhoarding will be relatively higher for less palatable than palatable seed species. The study species were *P. altissima* and *G. smeathmannii*, and the habitats were continuous forest (COR), forest edge (EDG) and extremely degraded riparian fragments (FRG). I found that seed removal rates were high and almost the same level in all three habitats for both species, but that seed fate differed among habitats. In the COR, more seed of each species was scatterhoarded than predated, but rates of scatterhoarding were higher for the less palatable *G. smeathmannii*. Distance seed was moved was approximately five times farther in the COR than in the EDG or FRG. I found strong evidence to suggest that the African pouched rat, *Cricetomys* sp., was responsible for the scatterhoarding.

The work in this chapter has been published: Aliyu et al. (2014) The interplay of habitat and seed type on scatterhoarding behavior in a fragmented Afromonate forest landscape. Biotropica 46(3) 264-267.

2.2 INTRODUCTION

Tropical forests are facing a seed dispersal crisis as dispersal networks are destroyed through anthropogenic drivers such as habitat degradation, fragmentation and hunting. Such changes affect forest composition and structure (Morris 2010; Harrison *et al.* 2013) so that for example, some regenerating forests may have a higher proportion of seedlings of small seeded (Vanthomme *et al.* 2010) or wind dispersed (Effiom *et al.* 2013) species than their ancestral plant communities. A recent meta-analysis of anthropogenic change on seed dispersal has shown that while different anthropogenic factors affect dispersal in various ways, large seeded plant species were always more vulnerable to such changes than small seeded species (Markl *et al.* 2012). However, irrespective of seed size, the disruption of seed dispersal is now recognised as a major threat to the future of many forests (McConkey *et al.* 2012).

Up to 70% of tropical forest tree species produce fleshy fruits that have evolved for dispersal by animals (Corlett 2007). This dependence of tropical forest trees on animals for dispersal makes them particularly vulnerable to frugivore decline and extinction (Corlett 2011; Fleming & John Kress 2011). Without animals' dispersers many tropical forest tree species will lose recruitment to high levels of seed predation and seedling competition under parent trees (Janzen 1969; Connell 1971; Harms *et al.* 2000; Chapman *et al.* 2010). Tree species with large fruit and seeds are most at risk because they depend on large bodied frugivores for dispersal (Schupp 1993) and these animal are more vulnerable to the effects of reduced habitat size, habitat degradation and hunting than small-bodied frugivores (Corlett 2007; Wright *et al.* 2007). However while predictions about the potential consequences of frugivore loss on seed dispersal are possible, particularly in the case of large seeded tree species (McConkey & Brockelman 2011), the actual effect of frugivore decline on any given plant species depends on the interplay of multiple factors (Galetti *et al.* 2006) because plant-frugivore networks are often nested within wider interaction networks which may build resilience into the system (Gilbert 1980). For example the loss of primary frugivores does not necessarily equate to a loss of dispersal because seed may be secondarily dispersed by abiotic means such as water or gravity or by scatterhoarding by animals (Vander Wall 1990; Vander Wall *et al.* 2005). Scatterhoarding refers to an animal behaviour whereby seed is collected during periods of abundance and stored for later consumption in scattered caches with just one or a few seeds in each (Vander Wall 1990). In the case of rodents, scatterhoarding has been described as a conditional mutualism (Bronstein 1994) in that an animal's behaviour

will depend on the environment, when food is scarce rodents act as predators but when food is abundant they may store some seed and act as mutualists (Theimer 2005). The specific fate of seed in such interactions may depend on the relative abundance of seed versus scatterhoarders density and the advantage to a seed of being cached versus left on the forest floor (Jorge & Howe 2009).

Scatterhoarding by rodents has undergone extensive investigation in Neotropical forests (Forget 1992; Jansen *et al.* 2012b), but the extent of scatterhoarding in African forests is largely unknown. The first record of rodents acting as dispersers in Africa was from Nyiramana *et al.* (2011),who showed that pouched rats (*Cricetomys kivuensis*) scatterhoarded large seeds of *Carapa grandiflora* from the forest floor in Rwanda. Midgley *et al.* (2012), demonstrated only very recently the potential of squirrels to scatterhoard large, hard seeds of marula (*Sclerocarya birrea*) from elephant dung in South Africa.

Since secondary dispersal by rodents may be a key to the future regeneration of large seeded forest tree species whose primary dispersers are in decline, understanding how the predation/dispersal ratio alters with fragmentation is crucial for effective forest management. Factors already known to interact and affect the fate of seed on the forest floor include seed size and palatability (Forget & Milleron 1991; Forget & Sabatier 1998; Forget *et al.* 2001; Chauvet *et al.* 2004) and degree of fragmentation (Farwig 2008; Cordeiro *et al.* 2009; Schleuning *et al.* 2011). While evidence points to more palatable seedsbeing more likely to be predated relative to unpalatable species, which may be preferentially hoarded, actual ratios depend on multiple factors, including food availability and rodent densities (Theimer 2005). The effects of forest degradation and fragmentation on predation/scatterhoarding ratios are complex and there are contrasting results in the literature. For example Jorge and Howe (2009) found ratios of predation to scatterhoarding in the large-seeded *Astrocaryum aculeatum* (Arecaceae) increased with fragmentation.

The overall aim of this chapter is to explore the way in which seed palatability and degree of forest degradation and fragmentation interacts to determine the fate of medium sized 28.4 (±0.43) mm x 26.5 (±0.38 mm in diameter) for *G. smeathmannii* and *P.altissima* 30 (± 0.33) mm x 15.3 (± 0.21) mm in diameter dispersed onto the forest floor by mammalian frugivores. Specifically I was interested in how seed characteristics and habitat affect predation rates and scatterhoarding in an Afromontane forest system.

I chose two medium-seeded (> 20mm in diameter) tree species with seed of different palatability to rodents and investigated the fate of this seed over three forest habitats from

core forest through forest edge to forest fragments. I had evidence that in the study area, forest edge degradation and forest fragmentation is accompanied by loss of both large bodied frugivores and tree species with large fruit (Ihuma 2007).

Testable hypotheses around context-dependent outcomes from this study include: i) the balance between predation and dispersal will favour predation in palatable seed speciesrelative to less palatable seed species and ii) in habitats where land use is such that fruit is scarce, such as fragmented and degraded forest, rodents will act more as predators than dispersers relative to habitats with an ample fruit supply.

2.3 METHODS

2.3.1 Study site

The study site was Ngel Nyaki Forest Reserve with two sites per COR, EDG and FRG habitat (see Section 1.2.1).

2.3.2 Study species

The study species (Section 1.2.2) had similar flowering and fruiting phenology and primary dispersal agents. Primates (*Pan troglodytes ellioti*, *Cercopithecus nictitans* and *Papio anubis*) swallow the fruits of both *P. altissima* and *G. smeathmannii* (Ihuma 2007). In addition many fruit were observed sucked by bats with seeds accumulating on the bare ground under bat roosts (P. M. Forget pers. comm.). Based on phylogenetic evidence e.g. molecular and hard seed coat characteristics, and observations of seed preference by caged rats, I propose that the two species differ in palatability to rodents, with *P. altissima* being preferred over *G. smeathmannii* has also been observed in other neotropical fruit species in both families (Chauvet *et al.* 2004).

2.3.3 Experimental design

The experiment included three habitats: i) riparian forest fragment (FRA), ii) forest edge (EDG), which was within 200 m of the grassland and iii) forest interior /core (COR) located at least 200 m within the forest from the forest edge.

Within each of the three habitats (COR, EDG and FRG) were two sites, at least 100 m apart, where adult trees of either or both *P. altissima* and *G. smeathmannii* were present.

Each site comprised of five plots of $1m^2$ in area, 25 m apart along a 105 m transect (Figure 2.1). Each 1 m^2 plot was split into four and within each of the four quarters of the plot; five seeds of each of the two species were placed on the ground after cleaning the plot, two at each corner and two in the centre. There were therefore 20 seeds of each of *P. altissima* and *G. smeathmannii* in each plot (plots were not set under parent tree). The grid design aimed at simulating primary dispersal of the key species by frugivores. Six Infra-red cameras were mounted abve six plots, two in each of the three habitats in order to capture image(s) of seed removers. The cameras simultaneously used an infrared sensor to detect movement by vertebrates which triggers the camera.The cameras lasted for five days above each of the six plots.

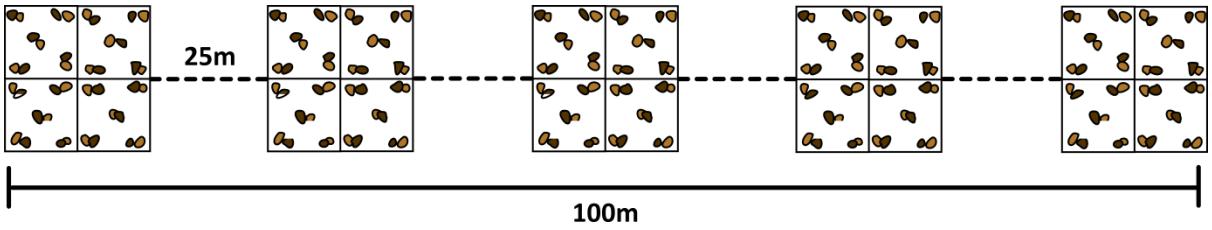

Figure 2.1: Experimental setup for *G. smeathmanii* and *P. altissima* seed removal. As illustrated, a pair of seeds (on of each species) was placed in the corners and centre of quadrats, spaced 25m apart along a 100 m transect.

Within the grid, each seed was marked with a white one metre long nylon thread following the method of Forget (1990) to aid in finding them. As the seed coat of *G. smeathmannii* was too thin to tolerate glue, the thread on these seeds was attached by drilling a hole through the seed and tying the thread round. This was feasible because the cotyledons are sufficiently robust that they do not break with drilling. In contrast the hard seed coat of *P. altissima* shattered when drilled but was hard enough to tolerate glue. To test for any effect of the two treatments, seed removal rates of glued versus drilled seeds were compared at FRA and COR. No difference in seed removal was observed.

Once set up, the grids were censused after five and ten days for seed fate, which was categorised into four classes: i) consumed (predation); ii) covered under the litter on the forest floor away from the plot (cached); iii) dug into soil to a depth of one to two centimeter whereby the seeds were covered and it was hard work to gently pull them out (buried); and iv) removed (fate unknown). Predated seeds were identified by having been partially

consumed or by the presence of a thread with no seed attached. Removed seeds were searched for within a 5 m radius which was then extended to 10 m if all seeds were not found. When a seed was found buried or cached a knot was made in the end of the thread. All threads from missing or eaten seeds were removed following the method of Forget (1996). The experiments were repeated two times, on the 27th April 2011 and 7th May 2011 for each species.

2.3.4 Data analysis

I was interested in seed fate, that is, the probabilities of seed remaining on the plot, being predated, cached or buried (dispersed) or missing and distance of dispersed seed in the different habitats (COR, EDG and FRG), and how seed species (palatable vs less palatable) affected fate. I fitted one mixed effects logistic multinomial regression model to examine the influence of seed species and habitat on seed fate. Additive random effects were fitted for plot, habitat and replicate variables. The multinomial probabilities of each seed fate were averaged over habitat * plot* replicate and were reported in terms of posterior means and a 95% credible interval (Bayesian analogue of a 95% confidence interval). The effects of species as well as species*habitat interaction were assessed by evaluating deviance information criterion (DIC) for the model with and without the above factors.

I fitted another mixed effects logistic multinomial regression model to examine the influence of seed species (palatability) and habitat (COR, EDG and FRG) on the response variable dispersal distance.I used a Bayesian bootstrap analysis (Xi 2005; Friedman *et al.* 2013) to estimate the median distance and the associated credible intervals for each species and habitat and to look for differences between them. Additive random effects were fitted for plot, habitat and replicate variables. As in the previous model the multinomial probabilities were averaged over habitat * plot* replicate and were reported in terms of posterior means and a 95% credible interval. I used DIC to evaluate whether considering the effects of species as well as species*habitat interaction improved the fit of the models.

The DIC reflects the goodness-of-fit of a model while penalizing for complexity (Spiegelhalter 2002). The smaller DIC value corresponds to the better model, and while a difference of 5-10 is suggestive, a difference of >10 indicates that the model with the smaller DIC is clearly statistically better. 100 000 iterations were run for each model, after the first 10 000 were discarded as a burn-in. The convergence was assessed visually.

The software R (R Development Core Team 2010) was used for additional posterior inference and graphs.

2.4 RESULTS

In Ngel Nyaki forest, I found that 15 out of the 16 images captured were of African pouched rats (*Cricetomys sp. nov* (Nesomyidae) (Olayemi *et al.* 2012), that means most or all seeds from the experimental plots were removed by a single rodent species.

Seeds were removed from each plot regularly, irrespective of habitat. After 10 days, of the total 2,400 seeds placed across all three habitats, 15 percent of *G. smeathmannii* and 20 percent of *P. altissima* seeds had been predated in the COR while 67 percent and 60 percent respectively were dispersed. The actual fate of the recovered seed in each habitat is presented in Table 2.1. The probability of any recovered seed being predated, cached, buried or missing after 5 and 10 days, as predicted from the mixed effects logistic multinomial regression model are presented in Figures 2.1a and 2.1b. As the conclusions drawn from the day five (5) and day ten (10) censuses were very similar, from here on in this chapter only the result of day 10 will be discussed. The model showed no evidence for any interactive effect between the species and habitat (ΔDIC = 2.76), but there were clear differences in seed fate frequencies among the three habitats (ΔDIC = 154.88), as well as between the two species (ΔDIC = 30.16).

Markedly more 'recovered' seed of both *G. smeathmanii* and *P. altissima* was dispersed (cached/buried) than predated in the COR (*P*=0.9999 for both species) and to a lesser extent in the EDG (*P*=0.9999 for *G. smeathmanii* and *P*=0.783 for *P. altissima*). For example, in the COR, after 10 days, 15% of *G. smeathmanii* and 20% of *P. altissima* seed had been predated, while 67% and 60% respectively were dispersed. In the FRG however, levels of predation of both species were much higher so that the difference between dispersal and predation was minimal for the recovered seed of *G. smeathmanii* (31% predated and 43% dispersed). This trend was reversed for *P. altissima* where 43% of seed was predated and only 30% dispersed (*P*=0.9962) (Fig 2.0).

Table 2.1: The fate of the recovered seed of *G.smeathmannii* (G) and *P. altissima* (P) in percentage in each habitat, forest core (COR), forest edge (EDG) and forest fragment (FRG) after day five and day 10.

Habitat	Species	Day	% Predated	% Cached & Buried	% Missing
COR	**G**	5	12	69%	19%
	G	10	15	67%	18%
	P	5	17	63%	20%
	P	10	20	60%	20%
EDG	**G**	5	27	43%	30%
	G	10	31	43%	26%
	P	5	40	33%	27%
	P	10	43	30%	27%
FRA	**G**	5	21	58%	21%
	G	10	24	53%	23%
	P	5	39	44%	17%
	P	10	38	41%	21%

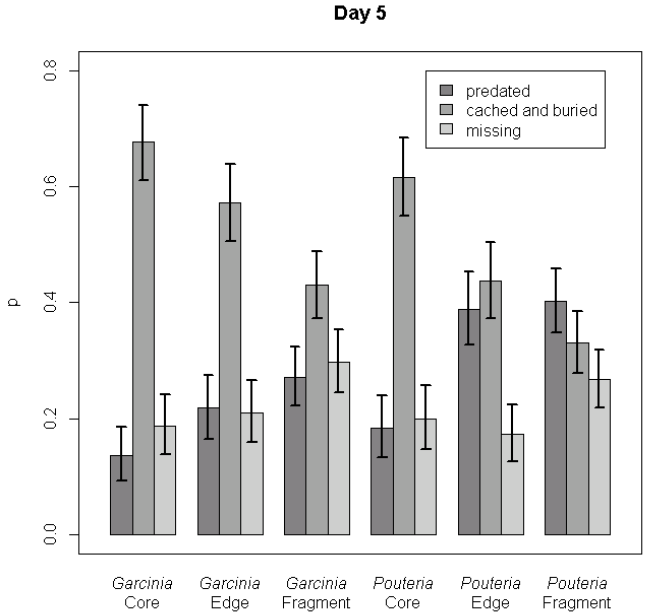

Figure 2.1a: The probability of any seed for both species (in each habitat) being predated, cached and buried or missing on day 5.

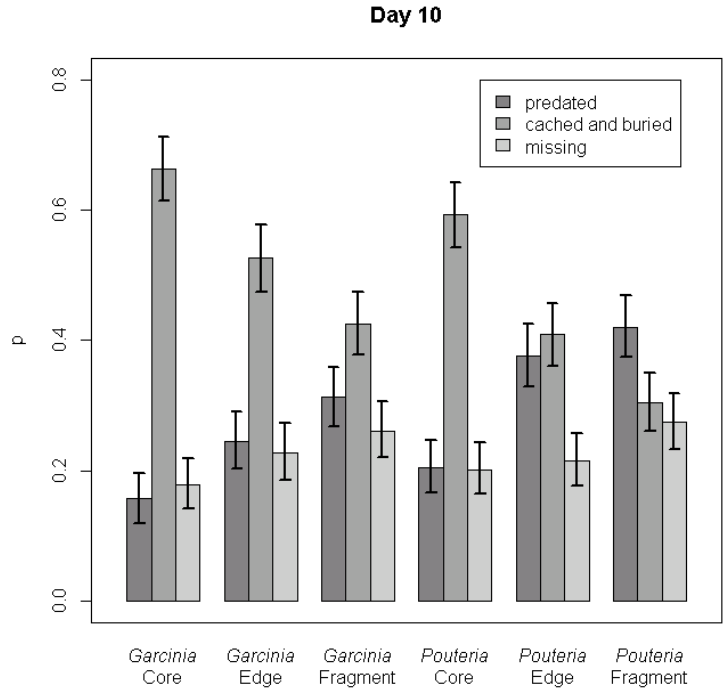

Figure 2.1b: The probability of any seed for both species (in each habitat) being predated, cached and buried or missing on day 10.

In terms of probabilities and mindful of the fact that values of *P* (Bayesian probability) closer to one indicate good support for the hypothesis (see data analysis above), I found that the probability of seed predation increased with habitat degradation (COR ≥ EDG ≥ FRG) for both *G.smeathmannii* (*P*=0.9824) and *P. altissima* (*P*=0.9110) , although *P. altissima* seedshad an approximately 40% higher probability of being predated than *G.smeathmannii* in all three habitats (*P*=.9608; Fig. 2.1b).

Rodents either cached seeds beneath the thick litter that covers the ground early in the rainy season or buried them 1-2 cm deep and covered the site with litter. The probability of seedsbeing hoarded in this way was markedly higher in *G. smeathmanii* than in *P. altissima* across all three habitats (*P*=0.9716) (Fig. 2.1b, Table 2.1) and in contrast to predation which increased with fragmentation *G. smeathmanii* (*P*=0.9976) and *P. altissima* (*P*=0.9824).For both seed species in each habitat, burying was more common than caching: *P. altissima* COR *P*= 0.0021; EDG *P*< 0.0001;FRG *P*< 0.0001; *G. smeathmanii* COR *P*=0.0439; EDG *P*<0.0001 and FRG *P*<0.0001 (Fig. 2.1a and b).

The observed dispersal kernels and estimated means with respective 95% CI are shown in Figure 2.2. The mean distance that seed was moved markedly decreased with increased fragmentation and degradation. On average the distance a seed was moved in the COR was 5.98 m but only 1.79 m and 1.07 m in the EDG and FRG habitats respectively (*P*=0.99 for both species). There was a small difference between the seed species in the distance they were moved. In the COR, the median caching distance for *G. smeathmanii* seeds was estimated to be 5.01 m which was the same (*P* = 0.738) as that of *P. altissima.* However, the rounding error involved when recording the data may make such small differences irrelevant.

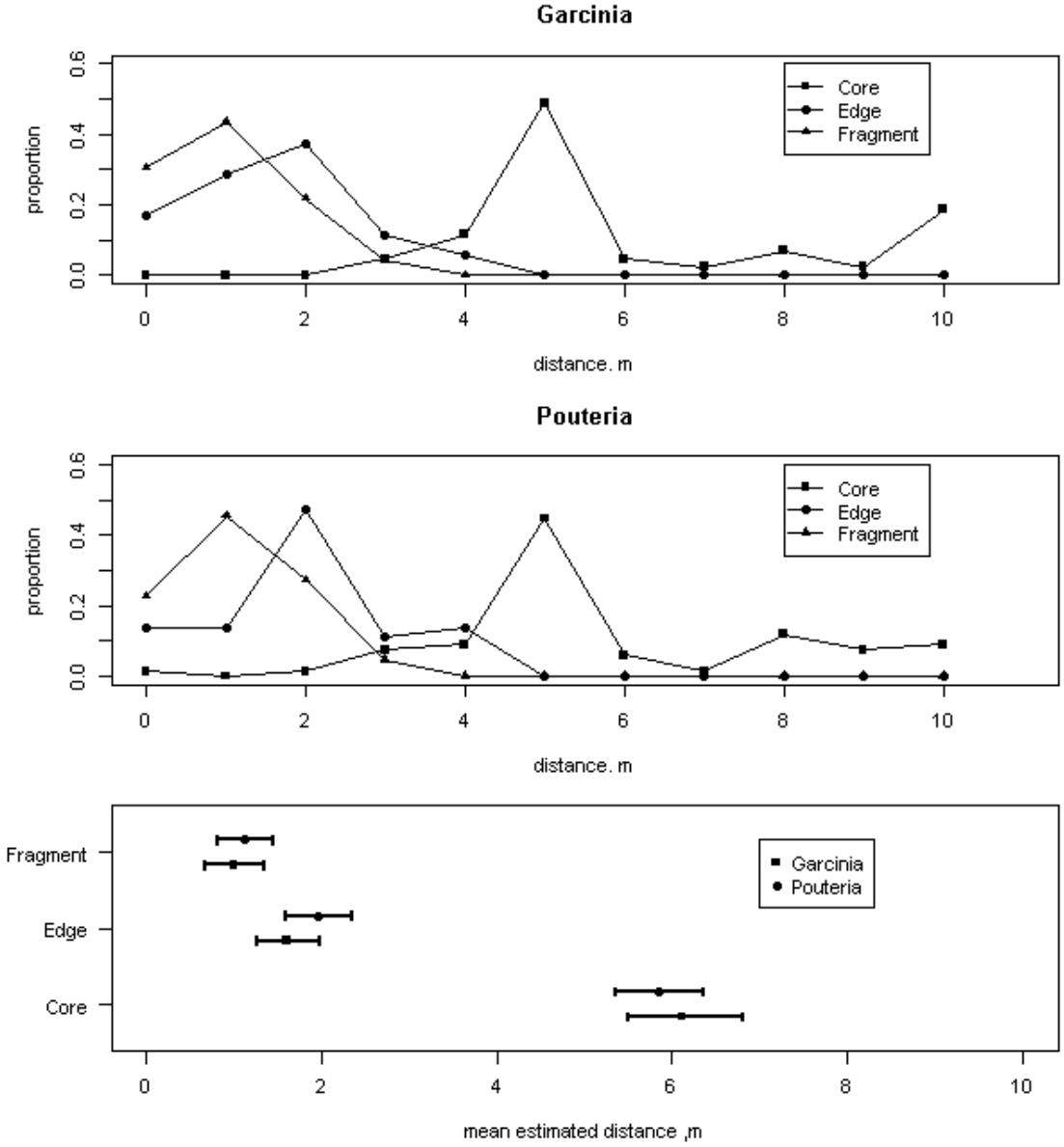

Figure 2.2: Dispersal patterns in *G. smeathmanii* and *P. altissima*. (Top) *G. smeathmanii* dispersal kernel in each habitat. (Middle) *P. altissima* dispersal kernel in each habitat. (Bottom) Average dispersal distances and 95% CI for each species per habitat.

2.5 DISCUSSION

This study is a major contribution towards understanding how the fate of large seed may change with increasing fragmentation and degradation of African forests. The results of this study demonstrate a shift in probable seed fate from dispersal to predation with increasing degradation and illustrate that seed characteristics such as palatability, can affect outcome.

2.5.1 Seed removal

Ninety four percent of all the seed of *P. altissima* and *G. smeathmanii* in the plots was removed within 10 days and rates of removal did not vary among habitats (COR<EDG or FRG). While high relative to comparable studies on rates of removal of large-seeded Neotropical species, (E.g. Forget 1996; Guariguata *etal*., 2002) removalrates may vary between seasons depending on food availability and this warrants further investigation at the Ngel Nyaki Forest Reserve. The fact that removal rates were extremely similar in all three habitats is explored below in the context of predation versus dispersal ratios. The main agent of removal seems to be the African pouched rat *Cricetomys sp. Nov* (Olayemi *et al.* 2012) because 15 out of a total of 16 images taken by infra-red cameras above six of the seed piles plots were of *Cricetomys sp. nov* eating or sniffing the seed. This is a significant finding in that it adds to the relevance of a report by Nyiramana *et al.* (2011) about *C. kivuensis* scatterhoarding large seeds in a Rwandan forest. The fact that this genus is widespread across the Guineo-Congolian forest block (Olayemi *et al.* 2012) suggests that it may play a major role in secondary seed dispersal in forests across this part of Africa.

2.5.2 Predation

As mentioned above, while rates of seed removal in this study were much the same irrespective of fragmentation or degradation, the probability of seed predation increased markedly with fragmentation in both seed species. This finding is concordant with the results of seed fate experiments by (Jorge & Howe 2009) for the large seeds of *Astrocaryum aculeatum* (Arecaceae) in Brazil and with those of Guariguata *et al.* (2002), for large seeded *Dipteryx panamensis* (Fabaceae) in Costa Rica. However it is clearly difficult to predict what the effect of fragmentation/degradation will be on seed predation rates because in their same study Guariguata *et al.* (2002) found that predation rates for the very large seeds of *Carapa*

*guianensis*were higher in continuous than fragmented forest. Moreover, Cordeiro *et al.* (2009) found no significant effect of fragmentation on predation rates of *Leptonychia usambarensis* (medium-sized seeds), and Farwig (2008) reported a significant decrease in predation of the small seeds of *Prunus africana* with increasing fragmentation. Clearly many factors interact to contribute to the final outcome of fragmentation/degradation on seed predation. In this study I found support for both of the hypotheses around predation, that is i) the balance between predation and dispersal will favour predation in palatablerelative to less palatable seed species and ii) in habitats where land use is such that seed is scarce, such as fragmented/degraded forest, rodents will act more as predators than dispersers relative to habitats with an ample seed supply. Another possible scenario to explain higher predation in fragments would be a greater abundance of rodents in fragments relative to continuous forest. Because rodent predators are more likely to decline through the effects of hunting and loss of habitat in degraded/fragmented areas than in continuous forest (Dirzo *et al.* 2007) rodents will increase in abundance. While I do have evidence for fewer fruiting trees in fragments (Ihuma 2007), there is no evidence to suggest more seed predators. As part of another project, over 50 individuals of *C. sp. nov* were trapped in the three habitats (COR, EDG and FRG (J. Thia unpubl. Data) but the success rate was higher in the COR than in the EDG and the FRG habitats.

The most parsimonious explanation for higher predation of *P. altissima* seeds relative to *G.smeathmanii* and the one I used in developing the first hypothesis was based on comparative studies of Neotropical *Moronobea coccinea* (Clusiaceae) and *Chrysophyllum lucentifolium* and *Manilkara huberi* (Sapotaceae) (Chauvet *et al.* 2004). As is the case for *M. coccinea*, the seed of *G. smeathmannii* has bitter yellow-to-orange latex which in *M.coccinea* has been shown to be relatively unpalatable to rodents (P.M. Forget pers. Obs.). In contrast Neotropical members of the Sapotaceae family have palatable and nutrient rich cotyledons, a hard seed coat (associated with a rich nutrient resource and show intense post-dispersal seed predation by rodents (Forget & Vander Wall 2001; Chauvet *et al.* 2004). Moreover as mentioned above, caged trials at Ngel Nyaki (B. Aliyu, unpubl. Data) showed a preference by *C. species nov* for *P. altissima* seeds.

2.5.3 Dispersal

When plant-frugivore mutualisms are threatened by frugivore decline, the wider interaction networks in which they are embedded become critical by building resilience into the system (Gilbert 1980). While rodents generally hinder regeneration through predation, under some circumstances they enhance regeneration through scatterhoarding (Forget 1993) and in forests that have lost their primary dispersers, scatterhoarding may be key to a species survival(Feer & Forget 2002) . Unfortunately, such mutualisms may break down just when they are needed most, e.g. in fragmented or degraded habitats, as observed in this present study.

Ngel Nyaki COR has suffered a severe reduction in frugivores but not to the same extent as the FRG. For example in the COR there is a small population of chimpanzees (Beck & Chapman 2004) and large populations of putty nose monkeys (*Cercopithecusnictitans*) (Gawaisa 2010), but visits to fragments by either species is very uncommon (Ihuma 2007). Both these primate species disperse *P. altissima* (Gawaisa 2010; Dutton 2012). Moreover dispersal by fruit bats of *G. smeathmannii* seed is more obvious in COR than in fragments (P. M. Forget pers. comm.). Yet it is in the COR that markedly more seed is scatterhoarded. Here I suggest that the abundance of seed dispersed in the COR forest floor satiates the rodents, leaving excess seed to be scatterhoarded (Forget *et al.* 2002). However, the extent to which predation increases with fragmentation varies with seed species, such that while both *G. smeathmannii* and *P. altissima* are likely to suffer dispersal limitation through predation and reduced primary production in fragments, *G. smeathmannii* is more likely than *P. altissima* to tolerate increasing fragmentation and edge effects because its seeds are not particularly palatable to predators; would- be predators become dispersers.

In addition to more seed being secondarily dispersed in the core, I found that dispersal quality (*sensu* Schupp1993) was higher in the COR than in FRG and the EDG in that seed was moved on average, five times further in the COR than the FRG. Theoretically the farther an individual seed is moved from a parent tree, the higher the likelihood of its survival because it ‘escapes’ from density dependent intraspecific competition and host specific parasites and predators (Janzen 1970; Connell 1971; Terborgh *et al.* 1993; Notman *et al.* 1996; Peres & Baider 1997).

2.5.4 Conclusion

In conclusion, this work confirms that scatterhoarding rodents play a role in the dispersal of large seed in African forests and that habitat and seed species influence their behaviour. While these preliminary results indicate that the effectiveness of rodents may be higher in COR than degraded forest, further investigations are needed to determine if this is always the case. Indeed, the understanding of scatterhoarding in African forests is only just beginning and many questions remain to be answered. Future works at Ngel Nyaki should investigate the shifts in rodent density across habitats, and compare this to rates of predation and ultimate fates of different seed species.

CHAPTER 3

The effect of fragmentation on *Carapa oreophila* (Meliaceae) seed dispersal by scatterhoarding rodents in the Ngel Nyaki Afromontane forest.

3.1 ABSTRACT

Anthropogenic pressure has lead to fragmentation of tropical forests and defaunation of local animal communities (particularly large-bodied vertebrates). Loss of large frugivore species may be highly detrimental to fruiting species that produce large-sized seeds. This is because in their absence there might be a lack of frugivore species that can efficiently disperse their seed. Here, the dispersal of *Carapa oreophila* is addressed in the context of an Afromontane forest that suffers from human-driven degradation and has lost large-bodied frugivores. *Carapa oreophila* has seed and fruit traits (no odour and not attractive) that suggest mega-faunal dispersal presumably elephants—but since these are no longer present at the study site (Ngel Nyaki Forest), can scatterhoarding rodents assume the role of effective dispersers (as observed in the Neotropics)? In the highly degraded riparian fragments, where resources are scarce, rodents act more as seed predators than dispersers, consuming the majority of seed, whilst in forest, there was a greater propensity to hoard. Furthermore, it was deduced that rodents are more likely to disperse seed in the middle of *C. oreophila*'s fruiting season when the abundance of seed is greater. Results therefore suggest that the benefit *C. oreophila* receive from scatterhoarding rodents as substitute dispersers at Ngel Nyaki is dependent on the habitat and the variance in seed abundance throughout the fruiting season; these effects thus modulate the role of rodents as predators or dispersers.

3.2 INTRODUCTION

3.2.1 The ratio between hoarding and predation

Scatterhoarding by rodents, whereby seedsare collected during periods of abundance and stored in caches for later consumption (Vander Wall 1990), has the potential to disperse seeds great distances and deposit them in sites suitable for germination (Vander Wall 1990; Jansen *et al.* 2012b). Seed characteristics such as size, nutrient content (Jansen *et al.* 2004; Vander Wall 2010) tannin levels (Wang & Chen 2011), and palatability (Feer & Forget 2002; Aliyu *et al.* 2014) can contribute toward a rodent's choice to either consume a seed immediately or stock-pile it for later consumption. Such manipulation of a scatterhoarder's behaviour is believed to be under selection (Vander Wall 2010), and opposing selective pressures from different granivore taxa may shape seed trait variation in a plant's population (Siepielski *et al.* 2010) .

However, as the intent of rodents caching seed is for their later consumption, tension exists in the role they play in plant populations: i.e. as antagonistic predators or mutualistic dispersers (Bronstein 1994; Vander Wall & Joyner 1998). At its simplest level, this relationship is believed to be driven by the relative abundance of seed versus rodents (as this affects the ability of scatterhoarders to find seeds, the probability that seeds will be hoarded, and subsequently their survival to germination), but other ecological factors may play important roles too (Theimer 2005). Thus the proportion of cached versus predated seed varies intra- and inter-annually (Jansen *et al.* 2004; Li & Zhang 2007; Nyiramana *et al.* 2011; Xiao *et al.* 2013), as does successful germination (Jansen *et al.* 2004), depending on the relative amount of crop produced in a given fruiting season. Furthermore, scatterhoarders differ in their potential "appetites' from frugivore dispersers; frugivores need only be satiated at the time of feeding while in contrast, because scatterhoarders handle more seed than they can eat at once, plants need to produce large enough crops to ensure that some seeds escape consumption in the future (Theimer 2005; Vander Wall & Beck 2012). Therefore when the abundance of available food sources are greater,scatterhoarders may choose to hoard seeds, as opposed to immediately consuming them (Jorge & Howe 2009; Haugaasen *et al.* 2010).

The ecological context in which the rodent-plant relationship occurs might also play a vital role in determining the role scatterhoarders assume (Theimer 2005). Fragmentation and degradation of forest may drive a scatterhoarder's behaviour from acting predominantly as a mutualist that disperses seed to an antagonist that consumes the majority of seed. Jorge and Howe (2009) demonstrated the ratio of predation to hoarding increased, and the distance of

seed moved decreased, from continuous forest to intensely fragmented forest in the Amazon. In a Nigerian montane forest, Aliyu *et al.* (2014) observed a similar pattern between continuous and degraded forest fragments. They also demonstrated that palatability of seeds can influence a scatterhoarder's decision to cache or consume a seed, in that seeds of the more palatable species *Pouteria altissima* were consumed more readily versus *Garciniasmeathmanii* (which had a greater propensity to be hoarded). Research on seed fate suggests that seeds in the forest edge may also suffer higher rates of removal and predation compared to the forest interior (Pinto *et al.* 2009).

3.2.2 Differences between Neotropic and Afrotropic seed dispersal

While scatterhoarding has been studied intensely in the Neotropics, little work has been done in the Afrotropics. It has been demonstrated that Neotropical scatterhoarders alter their home-range sizes with respect to the availability of food trees (Jorge & Peres 2005; Emsens *et al.* 2013), direct their foraging to where the probability of successfully finding food is high (Peres *et al.* 1997), and likely play a vital role in dispersing large-seeded tree species that almost certainly evolved for dispersal by now extinct mega-faunal mutualism (Guimarães *et al.* 2008; Jansen *et al.* 2012b). While some recent studies have emerged from the Afrotropics (Nyiramana *et al.* 2011; Aliyu *et al.* 2014), there remains gaps in our knowledge in understanding the absolute importance of scatterhoarding rodents to the recruitment dynamics of Afrotropical trees.

Unlike the Neotropics, where mega-fauna have been extinct since the Pleistocene, Africa still retains five mega-faunal genera: *Ceratotherium*, *Diceros*, *Giraffa*, *Hippopotamus*, and *Loxodonta* (Guimarães *et al.* 2008). Loss of very large vertebrate frugivores globally has led to the proposition of the so called "mega-faunal fruit syndrome" to account for failed seed dispersal in trees with exceptionally large seeds that do not appear to be primarily dispersed by extant taxa (Guimarães *et al.* 2008). Guimarães *et al.* (2008) propose that mega-faunal fruit syndrome can be inferred based on covariance in fruit and seed size: that is, a tree species is likely to have receivedmore dispersal benefit from mega-fauna (over extant taxa) if it produces large fruit with a single, extremely large seed.

3.2.3Carapa and large fruit dispersal by mega-fauna

Carapa (Meliaceae) is a Pantropical genus native to central and southern South America and the West Indies. However, its centre of origin is in West Africa (Kenfack 2008, 2011) where it occurs in lowland to montane forest: e.g. 2,600 m.a.s.l. in Rwanda (Nyiramana *et al.* 2011) and 2,400 m.a.s.l in Nigeria(Chapman & Chapman 2001) . It is an economically important genus (Forget & Jansen 2007) valued for its timber and oil which is extracted from its extremely large, lipid-rich seeds (Gueye *et al.* 2010; Weber *et al.* 2010; Prophiro *et al.* 2012). Fruit traits of this genus suggest adaptation and coevolution toward mega-fauna, in that trees produce large fruits with several chambers containing large seeds (Jordano 1995). Seed production in *C. procera* in French Guiana can vary dramatically between years (Forget 1996) but regular fruiting has been reported for *C. guianensis* in Brazil (Klimas *et al.* 2012). In the Neotropics, *Carapa* spp. are now dispersed almost exclusively by scatterhoarding rodents (Jansen *et al.* 2004). Dispersal rates (i.e. caching and burying) vary greatly within a single fruiting season (Forget 1996) and amongst years (Jansen *et al.* 2004) but are typically somewhere between 25−48% (Jansen *et al.* 2004).

Carapa evolved in Africa and all the 16 African species have large seeds (>20 mm in diameter)(Kenfack 2011) and may have evolved for dispersal by mega-fauna (Blake *et al.* 2009), so that recent mega-faunal mammal declines in Africa (Hawthorne 2000; Blake *et al.* 2009) could pose a potential threat to the regeneration ecology of *Carapa* in Africa. While it would appear African *Carapa* meet the criteria to be considered a potential victim of mega-faunal fruit syndrome, empirical evidence to directly support this is lacking. Elephants in montane West Africa are known to consume many large fruits including *Carapa* (Theuerkauf *et al.* 2000). However, the observation that seedlings of *C. grandiflora* were found throughout the Kilum-Ijim Forest (Cameroon Highlands, north-west Cameroon; where elephants went extinct approximately 100 years ago and are apparently dispersed by rodents) (Maisels *et al.* 2001) suggests that *Carapa* may be adapted, but not completely reliant on mega-faunal dispersal.

Yet the ability for rodents to truly assume the role of *Carapa* dispersers remains questionable. Given the effectiveness of a disperser is defined as the quantity and quality of dispersal (Schupp 1993), and given that rodents are most definitely unable to match the distance and quantity of dispersal achievable by mega-fauna, the true effectiveness of rodents as dispersers of large-seeded African trees needs to be addressed in light of declining mega-fauna populations. In the Nyungwe National Park, Rwanda—where forest elephants are now

extinct—Nyiramana *et al.* (2011) report very low levels of caching of *C. grandiflora* seeds (1.9 % and 2.8%), which are several orders of magnitude lower than have been recorded for *C. procera* in the Neotropics, or for species elsewhere that depend on scatterhoarding for dispersal (Forget *etal*., 2002) . Secondly, at the study site for this present work (Ngel Nyaki Forest, Nigeria), where forest elephants have been extirpated for at least 60 years (Hare pers. comm.), I have observed extremely low numbers of *C. oreophila* seedlings relative to adult trees (pers. obsv., see Chapter 1). Finally, seeds added to the forest floor at Ngel Nyaki and protected from predation by rodents germinate and grow (unpub. results), indicative of dispersal limitation rather than unsuitable habitat.

The overall aim of this study was to explore the fate of *C. oreophila* seeds deposited onto the floorof the three Ngel Nyaki forest habitats (COR, EDG and FRG; Chapter 1) in order to determine whether or not *C. oreophila* is being dispersed at Ngel Nyaki in the absence of any mega-fauana. From previous studies and observations in Ngel Nyaki (camera trap images), it is known that the most important (and possibly sole) disperser of *large seed (>20 mm)* in Ngel Nyaki is the African pouched rat*Cricetomys* sp. nov (Olayemi1 *et al.* 2012). Camera trap observations by Nyiramana *et al.* (2011) for *C. grandiflora* also support this genus as the singular secondary disperser of *C.grandiflora* in Rwanda.

The two main objectives of this study were to: i) determine how forest fragmentation and degradation affects the fate of *C. oreophila*seeds and ii)determine if these fates differed over the main six week fruiting season of *C. oreophila.*

Three hypotheses were tested: i) seeds in degraded/fragmented habitats will have a higher probability of being predated than in core forest because of reduced seed availability in forest fragments; ii) Within fruiting seasons the predation/dispersal balance will change, such that at the height of the fruiting season (when rodents are satiated) more seeds will be hoarded relative to the beginning and end of the fruiting season (when seeds are scarce). Finally iii) *C. oreophila* seeds at the onset/ending of the fruiting season experience high predation/dispersal ratios due to limited resources available to scatterhoarding rodents relative to the peak of the season when resources are more abundant.

3.3 METHODS

3.3.1 Study site

The study site and habitats (COR, EDG and FRG) are described in detail in Chapter 1 (Figure 1.1 and 1.3; Section 1.2.1)

3.3.2 Study species

The focal species of this study was the Meliaceae *C. oreophila* (see Section 1.2.2).

3.3.3 Phenology

In order to investigate fruiting patterns of *C. oreophila* phenology data (Nigerian Montane Forest Project records) from 2011 were collated. These data (from 25 C. *oreophila*individuals) were collected over 10km of regularly walked transects (4.0m wide = 20,000m^2) dispersed throughout the Ngel Nyaki Forest. These transects were established in 2006 using a systematic design (500m apart) (Beck & Chapman 2008) and since then have been walked on a monthly basis for tree phenology sampling. In this study, the phenology records were used to provide the number of *C. oreophila*trees fruiting per month to give an indication of fruit abundance; Jansen *et al.* (2004) found a correlation between the number of fruiting trees of *C. procera* and fruit abundance. Only trees >10 cm in diameter at breast height (1.4m) were recorded.

In order to determine whether 2011 was a rich, average or lean fruiting season for *C. oreophila* at Ngel Nyaki the results from the analysis described above were compared with the same analysis of over five consecutive fruiting years at Ngel Nyaki (NMFP phenology records).

3.3.4 The effect of habitat on seed fate

To test for the effect of habitat (COR, EDG and FRG) on seed fate, in each habitat two 100m-long transects (100m apart with five 1×1m^2 quadrats placed along its length, 25m apart) were set up to examine how many seeds were: (a) consumed (predation); (b) covered under forest floor litter away from the plot (cached) or dug into the soil (buried); or (c) removed but not locatable (fate unknown, i.e. missing); NOTE: both caching and burial are considered as “hoarded” in this study, because *C. oreophila* being large seed distinguishing

cached and buried seeds was difficult in Ngel Nyaki Forest Each quadrat was divided into four 0.25m^2 plots, and five fresh *C. oreophila* seeds were placed in each plot – one seed in the plot centre and one in each corner, *sensu* (Aliyu *et al.* 2014) (Figure 3.1). Deposition of seeds onto the forest floor was to simulate seed released from fruitsafter they had fallen onto the ground and split open, spilling seeds. A total of 800 seeds were used per habitat and 2,400 seeds in the entire experiment. Each seed was marked with a 1m-long white nylon thread following the method of Forget (1991) to aid in their location post-removal. Once set up, the experimental plots were evaluated for seed fate at two, five and 10 days. Removed seeds were searched for within a five m radius of plots, which was then extended to 10m if all seeds were not accounted for. Predated seeds were identified by having been partially consumed or by the presence of a thread with no seed attached. When a seed was found hoarded a knot was made in the end of the thread in order to avoid recording it twice. All threads from missing or eaten seeds were removed (Forget 1996).

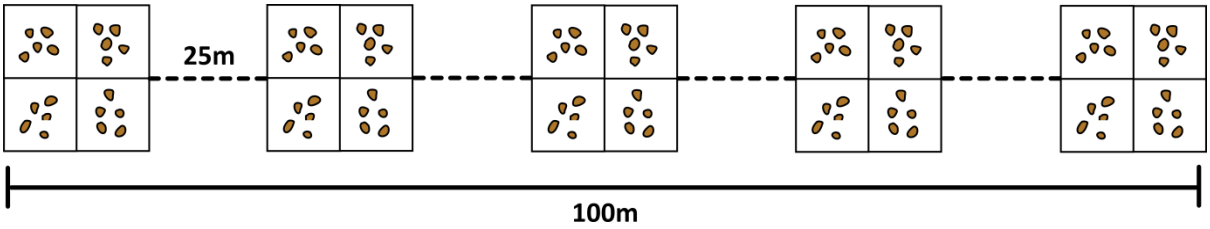

Figure 3.1: Experimental setup for *C. oreophila* seed removal. Five seeds were placed in one of four quadrats per plot.

3.3.5 The effect of seasonal variation on seed fate

To test for the effect of seasonality on seed fate the experiment was repeated four times during the fruiting season of 2011, from the very beginning of the season until there were insufficient seeds available to run the experiment. Each experiment ran for 10 days and there were four periods (S) during the season: August 18−28 (S1); September 5−15 (S2), 18−28 (S3); and October 2−12 (S4). At the end of each 10 day run the experiment was reset with fresh *C. oreophila* seeds, because seeds were removed rapidly within two to five days.

3.3.6 Statistical analysis

To determine the probability that a *C. oreophila* seed placed on the forest floor would be predated, hoarded (potentially dispersed), or go missing, in each of the four 10 day periods over the six week fruiting season, and in the three different habitats (COR, EDG and FRG), Bayesian statistics (Ellison 2004) were employed. A mixed effects multinomial logistic effects model was used, similar to that in Aliyu *et al.* (2014) as discussed in Chapter 2, which means results are directly comparable. The results of Bayesian analyses are presented in terms of posterior probabilities (*P*). *P* is the probability that a statement is true given the observed data. This is in contrast to the classical *P*-value, which is the probability of mistakenly rejecting the null hypothesis. Bayesian *P* values closer to one indicate that the hypothesis is well supported by the data (Agresti 2007).

3.4 RESULTS

3.4.1 Phenology

The percentage of *C. oreophila*trees with mature fruit in the transects during each month of 2011 is presented in Figure 3.2. Fruiting occurred all year round but there was a peak towards the end of the rainy season between early August and the end of September. Based on Nigerian Montane Forest Project phenology data from 2006 to 2011, the year of 2011 was deemed a rich and abundant fruiting year for *C. oreophila* at Ngel Nyaki.

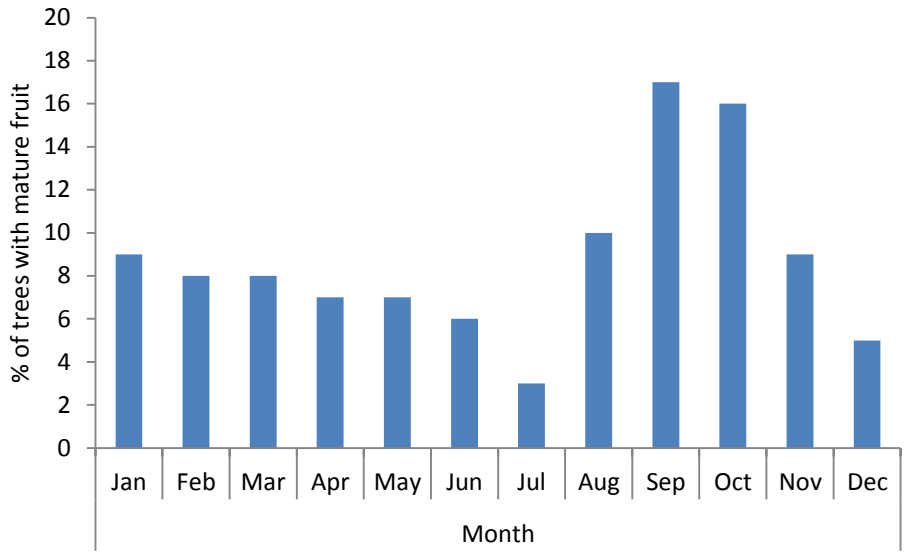

Figure 3.2: *C. oreophila* fruiting phenology during 2011. The bars represent the proportion of all 25 adult trees observed along transect that were fruiting in a given month.

3.4.2 Seed fate—the effect of habitat and season

Seeds were discovered and rapidly removed from all plots irrespective of habitat or fruiting period. Out of the 2,400 *C. oreophila* seeds used, after only two days at least 50% of seed had been removed from all plots across all habitats; by 10 days 100% of seeds had been removed from the EDG and FRG, and 98% from the COR. Of these removed seeds, 65% (1,562) were recovered and 35% (823) were missing. Of all the removed seeds 886 (37%) were predated and 28.3% (676) were hoarded (Table 3.1).

Table 3.1:2011 seed fates of *C. oreophila* seedsin percentages: predated seeds were consumed; missing seeds were those that could not be recovered; and hoarded seeds were either cached beneath leaf litter or buried in the soil. Each 10 day experiment was replicated over *C. oreophila*'s fruiting season at Ngel Nyaki (S1−S4).

Habitat	Season	Predated %	Missing %	Hoarded %	Remaining %
Core	S1	20.5	40.5	35	4
	S2	24	17	55	4
	S3	40	22.5	37.5	0
	S4	41	31.5	12	15.5
Edge	S1	19	61.5	19.5	0
	S2	42.5	10.5	47	0
	S3	47	24.5	28.5	0
	S4	34	31	35	0
Fragment	S1	17.5	70.5	12	0
	S2	54	24	21.5	0.5
	S3	57	27.5	15.5	0
	S4	46.5	34	19.5	0

Overall observation of the seed fates by days on average shows that the rates of seed predation consistently increased with fragmentation (P = 0.9604). The rates of hoarded seeds by rodents consistently decreased with fragmentation (P = 0.9864). The proportion of seeds missing increased from the COR to FRG (P = 9898);see Figure 3.3. The fate of seeds changed with variation in seasons in all habitats: after 10 days, higher proportion of seeds was lost in the first season (S1) than any of the other three seasons (P= 9999) (Table 3.1).

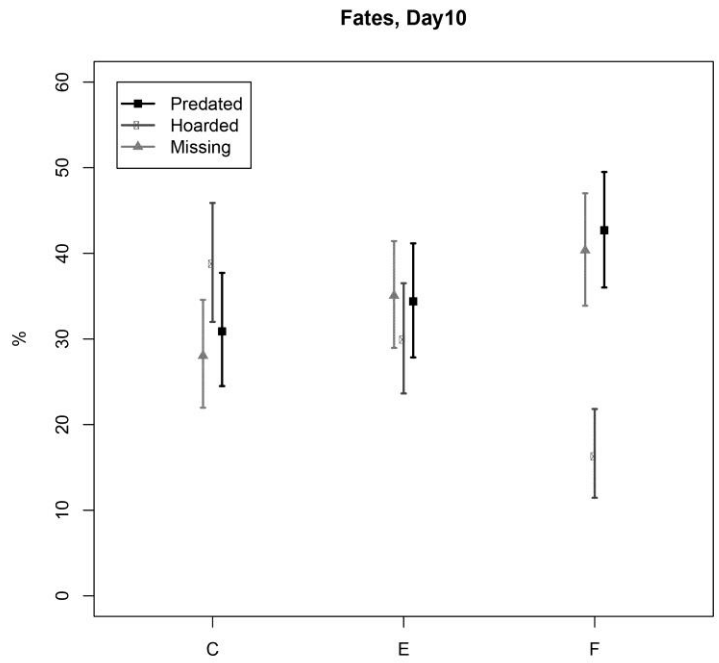

Figure 3.3: Percentages of seed predated, hoarded and missing after 10 days of seed placement on experimental plots in the three habitats.

3.4.3 Habitat and season interaction effects on seed fate

Markedly fewer seeds were predated in all three habitats at the start of the fruiting season (S1) than later on, but this was particularly so in the EDG (P = 0.999) and FRG ($P \geq$ 0.999). Seeds in the COR and EDG had a higher probability of being hoarded in the second fruiting period (S2) than either at the start of fruiting (P = 0.999) or towards the end of the season (S3 and S4; P = 0.999). While not as strong, the same trend was apparent in the FRG (P = 0.827).There was a particularly strong effect of fruiting period on the probability of seed going missing; in all three habitats a higher proportion of seeds was missing in the first period (S1) than in any of the later three periods (P >0.999). The interactive effect of habitat and season is depicted in Figure 3.4.

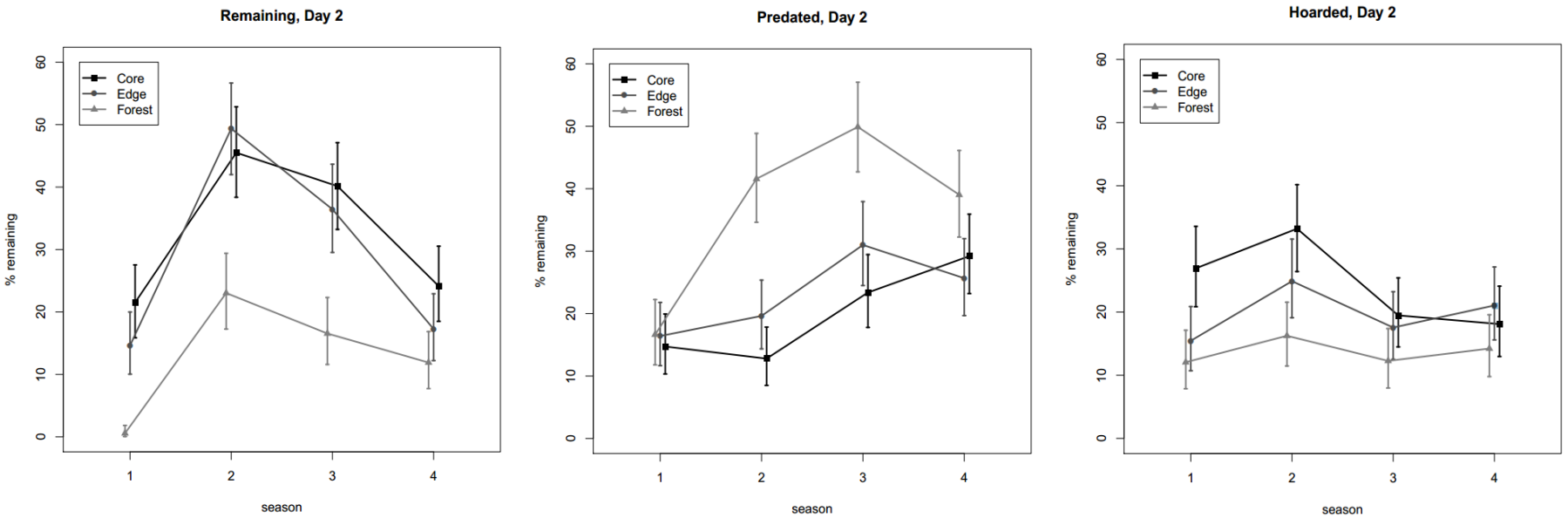

Figure 3.4: Interplay between seasonality and habitat on seed fate. Abundance of *C. oreophila* seed was greatest in the middle of the season (S2) and lower during the start (S1) and end (S3/4). Percent of seeds remaining (left), predated (middle), and hoarded (right) for each of the habitats ("core", "edge", and "forest" fragments) are given.

3.5 DISCUSSION

The objectives of this study were to understand how a scatterhoarding mutualism is influenced by temporal variation in seed abundance and habitat. The data suggest that intra- and inter-season variation and habitat drive changes in the behaviour of scatterhoarding rodents. This impacts the role they play as mutualistic dispersers and shifts it to one of a predator. The results of this study indicate that scatterhoarding rodents in montane Afrotropical forest may have more of an impact on seed rain relative to Neotropical counterparts.

3.5.1 Effect of fragmentation

While seasonal variation in seed abundance was an important factor contributing to *C. oreophila* seed fate, the most significant factor was habitat. On the Mambilla Plateau there is annual burning of the grassland surrounding forests by pastoralists, and cattle grazing occurs in the peripheries of the forest: these activities cause ecological damage to riparian fragment forest and the borders of large forest patches, like Ngel Nyaki (Chapman *et al.* 2004; Adanu *et al.* 2010). It was hypothesised that increasing degradation/fragmentation would lead to *C. oreophila* seeds in such sites having a higher probability of being predated than in continuous forest because of reduced seed availability. The density survey of *C. oreophila* adults showed relatively few adult trees in the EDG and even fewer in the FRG (See Chapter 1), and given the fragment forest around Ngel Nyaki contains few large-seeded tree species (Ihuma 2007), one might predict that any large seeds will exhibit high probabilities of predation and this was supported by my data(Table 3.1).

Surprisingly, and not entirely in support of the hypothesis, *C. oreophila* seed fate in the COR and EDG were not markedly different to each other. However, seed fates in the COR always differed more from the FRG than the EDG. Possible causes of these trends that require further testing include the possibility that rodents may have larger home ranges in the EDG and travel farther to find food (Godsall *et al.* 2014) or there may be alternative food sources in the EDG. Rodent density may be lower in the EDG, for example because of a higher density of predators (Asquith *et al.* 1997). Regardless, the results demonstrated a higher probability that rodents being predators of*C. oreophila* seed in the highly degraded fragments as opposed to in the forest (COR and EDG).

Fragmentation impacted seed fate in two major ways: (1) by creating a more rapid

removal rate of seed, and (2) lowering the probability of seeds being hoarded versus predated, relative to the forest habitats, across the fruiting season. The proportion of removed seed predated was markedly higher in the FRG except during the S1 period. However, it is likely that most 'missing' seed in the FRG was taken down burrows and eaten, based on the observation of string trailing from burrow entranceswhich was record as predated seed (see Nyiramana *et al.* 2011). Fragments are also very small, such that strings would have been easier to detect than in the forest had they been hoarded, so I feel the assumption that missing seeds in the FRG were eaten is justified; whereas in core forest where seeds were abundant missing seeds were assumed to be cached farther than 10 m. Markedly higher predation in the FRG versus the forest is in agreement with findings of several other studies (Cordeiro *et al.* 2009; Jorge & Howe 2009) and is most likely to be a consequence of limited resources. As a consequence, I surmise that *C. oreophila* should be highly seed limited in the FRG—and this is partially supported by the low density of juveniles observed in the fragment forest—and that under these degraded habitat conditions, *Cricetomys* rats are even less likely to fulfil the role of mutualists and instead act as antagonists. Such behaviour may cause "local extinction" of seed populations in fragments (Hulme & Hunt 1999).

3.5.2 Effect of season

The results of this study demonstrate that seasonality contributes to differences in immediate seed fate in *C. oreophila* at Ngel Nyaki. The general trend observed in all habitats was high removal rates in the early period of the season (S1), followed by dramatically lower rates of removal during the peak of the season (S2), ending with an increase in removal toward the end of the season as seeds became increasingly less abundant again (S3−S4). Removal of seed by rodents may be expected to decrease during episodes of abundance as predators become increasingly satiated (Theimer 2005; Xiao *et al.* 2005; Li & Zhang 2007), but studies suggest that local density of seeds can play an important role in removal rates as well (Hulme & Hunt 1999). Even though seed fates differed across habitats, the shape of the intra-seasonal trends was largely the same for each habitat.

Interestingly, the results of this study in the abundant fruiting year of 2011 were comparable to those of Jansen *et al.* (2004) and Forget (1996) during lean fruiting periods in each study. Jansen *et al.* (2004) reported 100% removal of *C. procera* within 10 days during lean years and Forget (1996) reported >90% removal over 20 days in the lean fruiting month of May. Of interest are the similarly high removal rates (>90% in six days) reported for *C.*

grandiflora in the large expanse of montane forest in Rwanda during the lean fruiting years of 2008 and 2009 (Nyiramana *et al.* 2011). It thus appears (from seed removal alone) that in the Ngel Nyaki's rich 2011 fruiting year, the probability of seeds being removed by rodents is very similar to that of lean fruiting years in lowland Neotropical forest and extensive expanses of montane forest in Rwanda.

Such results do not bode well for secondary dispersal at Ngel Nyaki, because seedling survival is higher following predator satiation (Li & Zhang 2007; Vander Wall 2010), and if rodents at Ngel Nyaki are never satiated, they are less likely to act as dispersers. However seed removal alone is not necessarily a good predictor of seed fate (Xiao *et al.* 2013), and it is thus important to consider what specifically happens to each seed. Averaged over the entire fruiting season, the proportion of removed seed predated in the COR (32%), was high compared with predation of *C. procera* in rich fruiting years (14%) and even lean years (23%) in French Guiana (Jansen *etal* 2004). Such high immediate predation rates of *C. oreophila* in Ngel Nyaki, relative to the lowland Neotropics, again suggest seed limitation could constrain *C. oreophila* recruitment within this forest.

Taken together, the seed fate census in Ngel Nyaki's COR suggests a low probability of effective seed dispersal; even in rich fruiting years a high proportion of seed is rapidly removed from the plot and predated. Under these conditions it is highly likely that cached seeds will be removed and also ultimately predated (Jansen *et al.* 2004). By mid-August to October when this study was carried out, *C. oreophila* was one of the few large-seeded species fruiting in Ngel Nyaki. *Cricetomys* rats have shown to be strong seed predators of Ngel Nyaki's large-seeded and small-seeded trees: e.g *P. altissima*, *Syzygium guineenseTrilepesium madagascariense* (Dutton *et al*., 2014), and *A. noldeae* (pers. obsv.). Despite high numbers of *C. oreophila* individuals in the COR, it seems that they are not producing sufficient seeds to satiate the rodents at this time of year. Despite 2011 being a prolific year for *C. oreophila*, not all trees fruited and fruiting was asynchronous.

Predator satiation promotes seed survival (Vander Wall 2010) and may even be essential for effective dispersal by scatterhoarding rodents. For example, in a rich fruiting year, Jansen *et al.* (2004) found that the probability of *C. procera* seedlings establishing from caches was only 0.7% and this was 13 times the seedling establishment of cached seeds during lean years. While further research is required with greater emphasis on rodent density and total available resources, it appears that the fruiting phenology may be a disadvantage for *C. oreophila* in terms of secondary seed dispersal by rodents.

3.5.3 Conclusions

This study has produced valuable insights into the vulnerability of species that, until recently, may have been entirely dependent on mega-fauna such as elephants for primary dispersal. While in the Neotropics (and elsewhere where there has been a long history of mutualism between rodents and tree species) rodents have selected for mast seeding (which leads to some seed dispersal), it may be that in the Afrotropics, where elephants (mega-fauna) are exhibiting major local extirpation, there is an ecological gap forming. Scatterhoarding rodents may thus represent a means of compensating for the loss of large-bodied frugivores in the Afrotropics—as demonstrated in this study. However, trees species with large, nutritious seeds—like *C. oreophila*—may exhibit variable benefits from rodent secondary dispersal depending on the ecological context the interaction between plant and animal occurs in.

CHAPTER 4

Seed fate changes with fragmentation and degradation in Afromontane forests: pre and post germination filters to recruitment establishment

4.1 ABSTRACT

Community composition of Afrotropical forests is changing in the face of degradation and fragmentation. Frugivore decline is leading to somewhat predictable changes in seed dispersal patterns and is a major driver of change. Less is known about a) the potential for secondary dispersal by rodents to compensate for frugivore loss and b) post dispersal establishment filters, yet understanding these processes is vitally important in forest restoration and management.

The aim of this study was to explore post-dispersal filters to the establishment of large seeded forest tree species and determine if seed burial (simulating rodents scatterhoarding) increases the probability of seedling establishment. The main questions were how do forest degradation and fragmentation (habitat) interact with seed species and seed treatment (exposed or not to mammalian predators and buried or not) to determine the probability of establishment to two years.

A multifactorial experiment was used to answer these questions. The experiment included five large-seeded species (*Anthonotha noldeae*, *Carapa oreophila*, *Garcinia smeathmanii*, *Pouteria altissima*, *Syzygium guineense*), three habitats of increasing degradation and fragmentation and four treatments; i) seed on forest floor and caged to exclude mammalian predators/herbivores; ii) seed buried to simulate caching by rodents and caged; iii) seed on forest floor, uncaged and iv) seed buried and uncaged. The study revealed six seed fates: seed death by seed mammalian predation or pathogen attack, seedling death by herbivory, pathogens or desiccation and seedling survival to two years. The experiments showed that the mammalian predation was the strongest filter to establishment across all species. No habitat was environmentally unsuitable for establishment, however habitat and treatment effects differed among species so that the probability of establishment was species specific and was determined by habitat and treatment interactions.

Given the intensity of mammalian seed predation, I propose that reforestation efforts should concentrate on seedlings grown *ex situ* to be replanted into the forest.

4.2 INTRODUCTION

Forest fragmentation and degradation have far reaching consequences for tropical biodiversity (Schleuning*etal*., 2011). While tree species diversity is not necessarily lost through fragmentation, species composition may change which in turn impacts community structure (Morris 2010). For example, fragmentation together with other types of habitat loss and hunting particularly affect large mammals (Laurance *et al.* 2002; Kosydar 2010), many of which are important dispersers of large seed (Corlett 2007). In contrast, small mammalian seed predators may increase (Asquith *et al.* 1997) or decrease (Corlett 2007) in abundance in fragments or their behaviour may change from mutualists to predators (Jorge & Howe 2009). Changes such as these directly impact seedling recruitment (Bricker *et al.* 2010; Norghauer & Newbery 2010; Clark *et al.* 2013). For example, dispersal limitation (Turnbull *et al.* 2000) following fragmentation is the main cause of regeneration failure in *Leptonchia usambarensis* in Tanzania (Cordeiro & Howe 2003; Cordeiro *et al.* 2009). However, loss of primary dispersers may sometimes be partly compensated for by secondary dispersers such as scatterhoarding rodents who move seeds and bury some below the soil surface, in the vicinity of fruiting trees (Forget 1996) as is the case at the study site, Ngel Nyaki (Aliyu *et al.* 2014).

As important as seed limitation (or indeed, sometimes more so) is establishment limitation (Clark *et al.* 2013). This occurs when biotic or abiotic factors are such that microsites into which seed are dispersed are unsuitable for successful seedling establishment (Nathan & Muller-Landau 2000). For example, seed predation and seedling herbivory (Janzen 1970; Makana & Thomas 2005), pathogen attack (Augspurger 1984) and microclimate effects, such as soil type, light levels, leaf litter (Hall 2008) and moisture (Veenendaal *et al.* 1996; Poorter & Hayashida-Oliver 2000), can all critically affect seedling establishment.

Species respond differently to potential threats to establishment: seed size and seed/seedling physiology interact with the environment to determine seed fate, such that it is difficult to accurately predict the final filtering effects of fragmentation/degradation on the seed rain in any one location (Clark *et al.* 2013). However, it is important to try and predict outcomes because fundamental changes in community composition following fragmentation and degradation may create feedback loops in carbon sequestration (Houghton *et al.* 1991; Grace 2004) and even climate change (Bagchi *et al.* 2014). Moreover the trajectories of passive forest restoration may be affected (Barnes & Chapman 2014), and complex cascading

feedback effects between genetic and ecological traits in tree populations can be set in motion through forest fragmentation (Jacquemyn *et al.* 2012).

Preliminary investigations in the study area, Ngel Nyaki Forest Reserve, in north east Nigeria have suggested altered recruitment patterns following forest degradation and fragmentation over the past thirty years (Chapman *et al.* 2004). I noticed some very severe discrepancies between adult tree species composition and that of juveniles which varied with habitat and were more extreme in some species than others (Aliyu unpubl. data). One reason for these apparent mis-matches may be local extinction/functional extinction of frugivores.

At Ngel Nyaki hunting has removed elephants and severely depleted the chimpanzee population (Chapman *et al.* 2004) which likely affects regeneration of the large-seeded species *Carapa oreophila* and *Pouteria altissima*,which are now dispersed by the pouched rats (*Cricetomys* sp. Nov) (Olayemi *et al.* 2012). These rodents may now compensate for this loss to some extent by scatterhoarding seeds of these species (Aliyu *et al.* 2014), but the exact benefit these species gain from being handled by rodents has not yet been quantified.

In light of this, the overall aim of this study was to explore the effect of species (seed traits) and the consequences of habitat degradation on seed fate in order to understand the factors responsible for filtering seeds and seedlings from the recruitment cohort. The study objectives were: i) to know the relative contribution of pre-germination (seed predation and seed pathogen attack) versus post-germination (seedling herbivory, seedling pathogen attack and desiccation) fates on seedling survival and the probability of seeds of each species in each habitat surviving after two years; and ii) to test for the effect of treatments (caged and un-caged) and seed burial on all of the above seed fates because burial may protect seeds from invertebrate and vertebrate predators.

4.3 METHODS

4.3.1 Study site and habitats

The study site and habitats (COR, EDG and FRG) are described in detail in Chapter 1 (Figure 1.1 and 1.3; Section 1.2.1)

4.3.2 Study species

Five moderate- to large-seeded species were chosen for this study based on their general need for vertebrate-assisted dispersal: *Anthonotha noldeae*, *Carapa oreophila*, *Garcinia smeathmanii*, *Pouteria altissima*, and *Syzygium guineense* (see Section 1.2.2).

4.3.3 Experimental design

In each of the three habitats, three replicate sites were selected at least 200 m from each other (Figure 4.1). In each site, a multifactorial split plot design was established at least 15 m away from focal species to understand how: (a) limiting seed removal by mammals, and (b) the type of seed deposition (surface or buried), impact the probability of a seed (i) germinating and (ii) becoming an established seedling? Four plots were set up, Two plots were caged (mammalian exclusion) while the other two were uncaged. The mammalian exclusion (U = un-caged, C = caged) was achieved by placing cages that were 80cm tall and 1×1 m^2, covered in 0.2×0.2cm wire mesh, and buried 10cm below ground, around the plots. Seed within a plot were either placed on the surface of the soil, or buried beneath it (S = surface, B = buried). The purpose of this treatment was to understand differences in seed fate between those seeds which land on the forest floor versus those which are handled and possibly buried by scatterhoarding rodents (Figure 4.1).

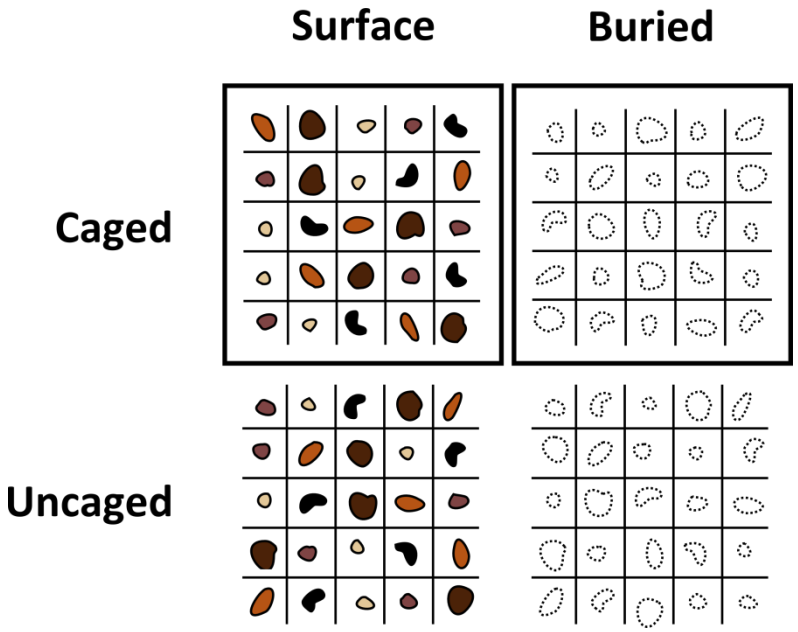

Figure 4.1: The four experimental treatments for every possible combination of species, buried vs surface, open vscaged. Five seeds of each species were used in each plot, summing to a total of 180 seeds per species. Seeds were added to the plot as they became available (see text).

The experiment was set updуring the peak fruiting period for each of the five focal species (*P. altissima*, *G. smeathmanii* and *A.noldeae* in April, *S. guieense* in May and *C. oreophila* in early August 2011; Figure 4.2a). Seeds were collected from mature fruits from approximately five trees per species. Seeds from the fleshy fruit were hand cleaned and all seedswere checked for insect infestation or growth of fungi, any seed with such sign was discarded. Seed viability was not tested given the fact that damaged seeds were discarded. The same day that the seeds were collected and cleaned they were sown (approximately 1cm deep; "secondary dispersal" treatment) or placed on the surface ("primary dispersal" treatment) in each of the plots (Figure 4.2b). The plots were set up at about 15 m away from parent trees.Seeds were spaced one each in 20×20 cm^2 within a 1×1 m^2 (Fig.4.1). Within each row was one of each species, to create some sort of randomization and mixing between seeds and future seedlings. The plots were monitored weekly for a period of 72 days(by which time all seeds had either died or germinated) after the start of the experiment for seed fates, which were: i) predation by mammals, and ii) death by pathogens/desiccation, or iii) germination. Following germination, seedlings were then scored for a following two years for one of six possible fates: I) Lethal pathogen attack before first leaf development, II) death by fungal pathogens, III) death by mammalian herbivory,IV) death by insect herbivory, V) death by

desiccation, or VI) establishment (Figure 4.2c).

Figure 4.2: (a) Experimental plots (caged and uncaged) for investigating filters to establishment. (b) A *G. smeathmanii* seed on the soil surface. (c) Establishment of seedlings in an experimental plot.

Seeds handled by scatterhoarders were recorded as being removed by mammals if they were either found chewed and eaten, or removed (but not locatable), from the plot. A seed was recorded as germinated when the shoot first became visible for seeds placed on the soil surface or when the shoot first appeared above the ground for buried seeds. Lethal pathogen attack before first leaf development was when the cotyledons were covered in fungus before true leaves appeared. Desiccation of seed was classed as the drying and resultant death of a seed before first leaf development or when the cotyledons dried up. Pathogen attack of seedlings was reported as a wilting or patchy discolouration of the seedling, sometimes the leaves were covered in fungus or other visible lesion. When insects consumed leaves to the point where seedlings died it was recorded as insect herbivory. Leaf and shoot removal or seedling uprooting was scored as mammalian herbivory. Seedlings were considered desiccated when their leaves remained brown and clearly dried up after several observations. Seedling height was measured to the nearest centimetre and leaf number was counted. Any seedling without leaves were considered as dead and after 2 years seedling less than 10 cm in height were not considered as successfully established.

4.3.4Data analysis

The aim of this study was to determine how habitat (COR, EDG and FRG) and treatment (C/S, C/B, U/S, and U/B) singly and through interaction affected the probability of seeds of five different forest tree species being established. I wanted to know the probability of these seeds germinating (surviving seed predation) and establishing after two years. Since the seed fate is a categorical variable, a logistic multinomial mixed-effects linear regression was applied. The model took into account both the fixed effects (species, habitat, treatments) and the random effects (plots). It was fitted within the Bayesian framework using the WinBUGS software (Spiegelhalter *et al.* 2002). A total of 105,000 iterations were run with the first 5,000 discarded as a burn-in. Every 20^{th} iteration was then recorded and used in the posterior analysis. The convergence was assessed visually. Posterior estimates of means as well as the 95% credible intervals were obtained for parameters of interest.

The model comparison was based on the Deviance Information Criteria (DIC) (Spiegelhalter *et al.* 2002). Smaller DIC values correspond to the statistically better models. When comparing two models, a difference (ΔDIC) of 5 to 10 is considered substantial, whereas a ΔDIC of over 10 would definitely rule out the model with the higher DIC. Based on the model, posterior probabilities were computed for various statements of interest(the seven seed fates). The software R (R Development Core Team 2010) was used for additional posterior inference and graphs.

4.4 RESULTS

4.4.1 General trends in seed fates

Given the large number of factor combinations in this experiment (three habitats, four treatment combinations, and five species), the results of this study are complex. However, by generalising the responses (seed fate) over factors, it is possible to draw broad conclusions about the variables that govern regeneration processes at Ngel Nyaki.

Seed fate probabilities varied with habitat (Fig. 4.3): The probability of seed removal by mammalian predators increased with degradation/fragmentation, while the probability of seeds dying from pathogen attack was highest in the COR and comparable between EDG and FRG). Seedling mortality in each of the habitats exhibited different probabilities for each fate, but generally speaking, there appeared to be a greater probability for seedling in the COR and FRG to establish after two years versus the EDG.

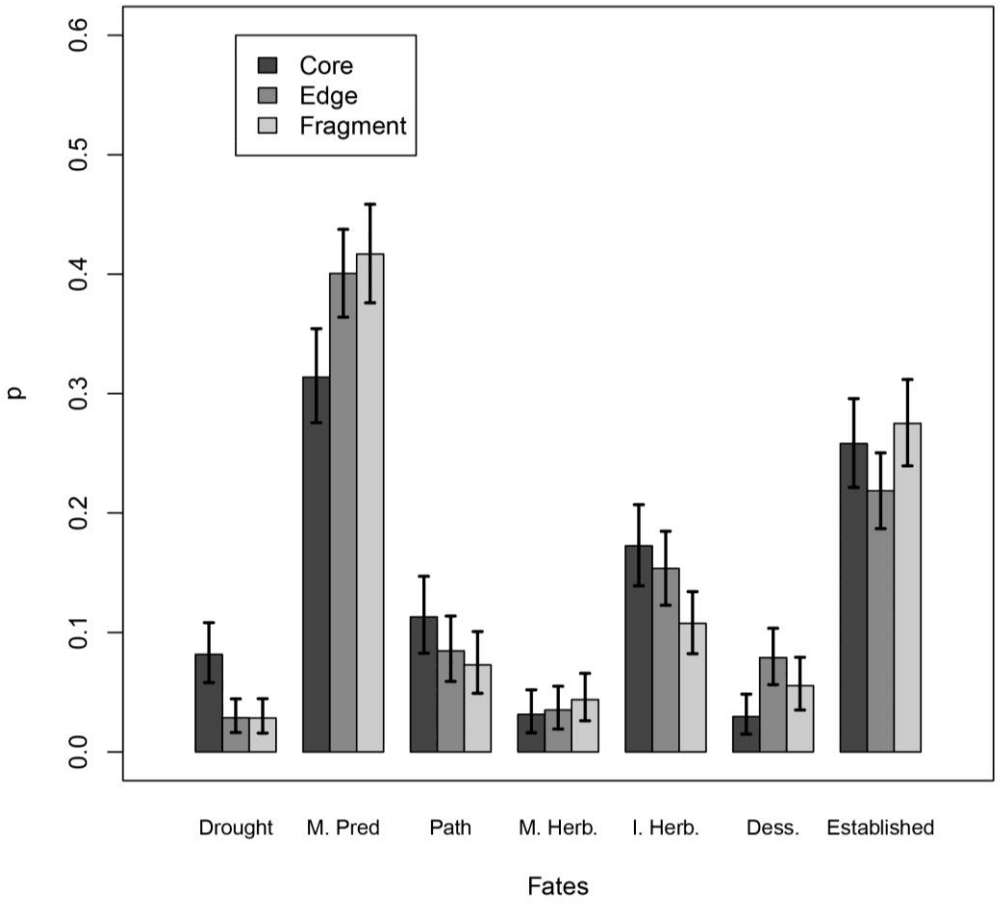

Figure 4.3: Fate probabilities per habitat (generalised over treatment and species) with 95% CI. Seed fates: seed desiccation or pathogen attack ("Desc./Path."); removal by mammals ("M. Pred"). Seedling fates: pathogen attack ("Path"); mammalian herbivory ("M. Herb."); insect herbivory ("I. Herb."); desiccation ("Dess."); two year survival ("Established"). *P* represents the probability of a particular fate in that habitat.

My seed treatment factor (un-caged versus caged, and buried versus unburied) was used to (1) simulate secondary dispersal by rodents, and (2) understand how exclusion of mammals impacts establishment of seedlings (Figure 4.4). The greatest effect observed amongst the different treatments was their impact on seed removal by mammals. Seeds that were un-caged overall exhibited much higher rates of removal than those that were caged. Furthermore, regardless of whether a seed was protected by a cage or not, those that were buried exhibited lower probabilities of removal than those that were on the surface. Cages also reduced the probability of seedlings succumbing to mammalian herbivory, but there was

increased probability of seedlings being eaten by invertebrates in caged plots. Desiccation/pathogen attack of seeds, or pathogen attack or desiccation of seedlings showed no clear trend amongst the treatments. Overall, seeds that were in caged plots had far greater probabilities of establishment after two years than those in un-caged plots.

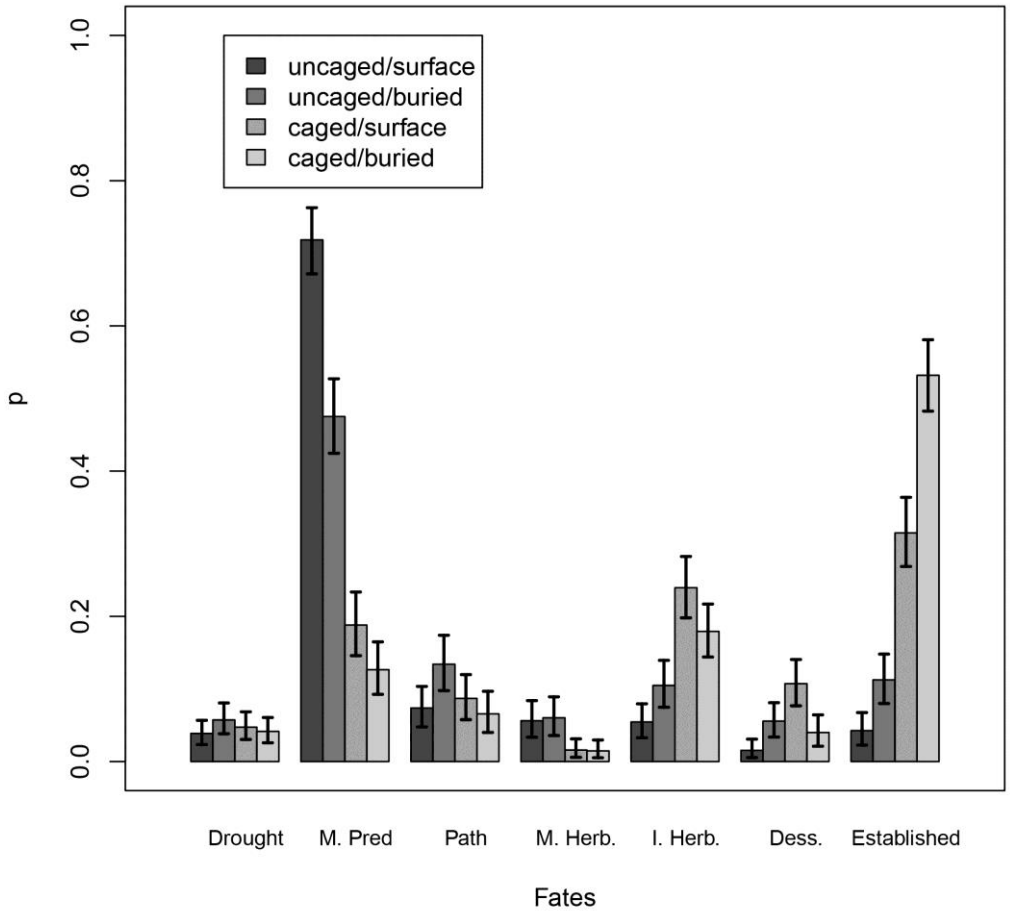

Figure 4.4: Fate probabilities per treatment (generalised over habitat and species) with 95% CI. Seed fates: seed desiccation or pathogen attack ("drought"); removal by mammals ("M. Pred"). Seedling fates: pathogen attack ("Path"); mammalian herbivory ("M. Herb."); insect herbivory ("I. Herb."); desiccation ("Des."); two year survival ("Established"). *P* represents the probability of a particular fate in that treatment.

Seed fates for each species varied widely (Fig. 4.5), though overall, removal of seed by mammals accounted for a significant portion of a seeds fate probability (>20%). This was particularly high for *C. oreophila* which exhibited seed removal probabilities of >60%. These removal probabilities likely reflect preferences: *C. oreophila>A. noldeae>G. smeathmanii>P.*

altissima>*S. guineense*. All other causes of mortality to seedlings and seed paled in comparison to that of mammalian removal in all except *S. guineense*. Not only was *S. guineense* the least likely to be removed from the plot but it observed markedly high seedling pathogen attack and insect herbivory probabilities. Thus, while mammalian removal largely appeared to influence establishment probabilities in the other four species, *S. guineense* establishment may be more constrained by mortality to seedlings.

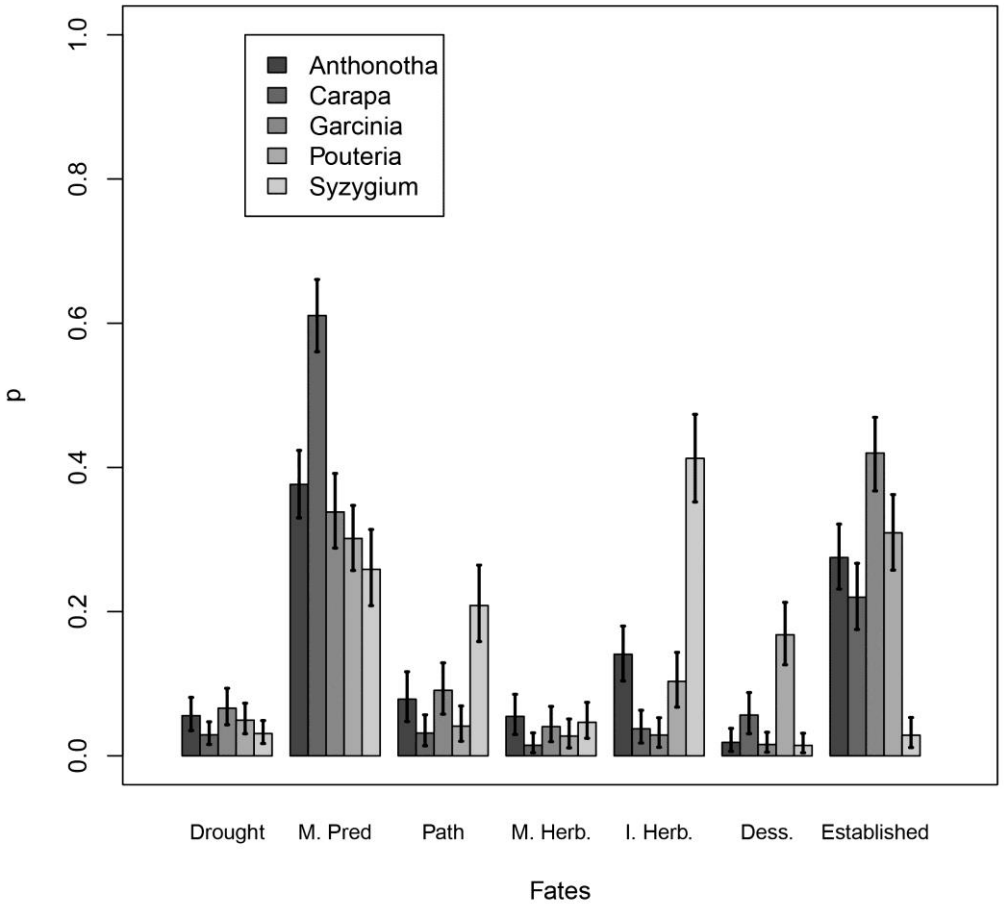

Figure 4.5: Fate probabilities per species (generalised over habitat and treatment) with 95% CI. Seed fates: seed desiccation or pathogen attack ("drought"); removal by mammals ("M. Pred"). Seedling fates: pathogen attack ("Path"); mammalian herbivory ("M. Herb."); insect herbivory ("I. Herb."); desiccation ("Dess."); two year survival ("Established"). *P* represents the probability of a particular fate for that species.

Finally, the disparity between germination and establishment success probabilities between species in each of the habitats (generalised across treatments) was assessed (Fig. 4.6). In all cases, establishment was lower than the probability of germination, though the actual difference varied with species and habitat. While *C. oreophila* had the lowest likelihood of germination (regardless of habitat), establishment of seeds in the EDG and FRG were comparable to other species. A major anomaly was *S. guineense*, in that although seeds had a very high probability of germinating in any habitat, survival of resultant seedlings to the two year mark was extremely low (<10%).

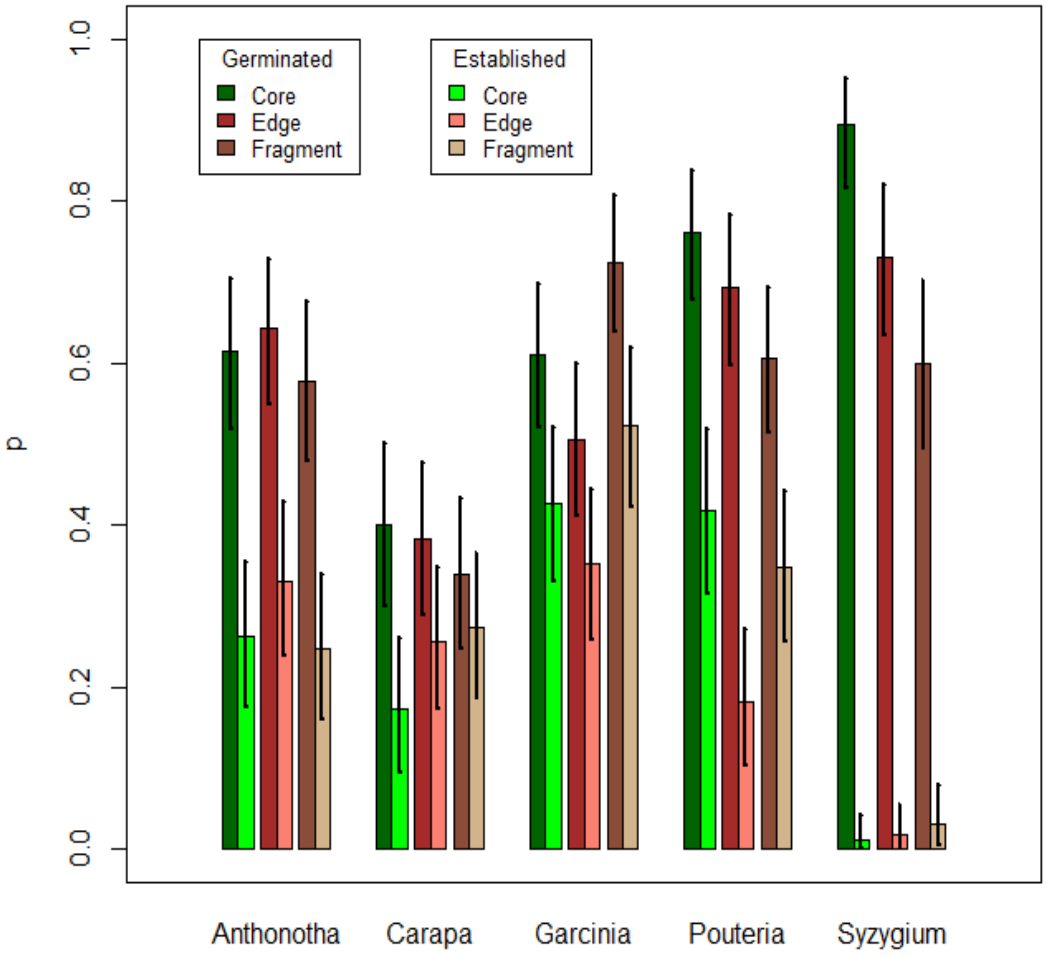

Figure 4.6: The probability of successful germination and establishment for each species in each habitat (averaged over all treatments) with 95% CI. The probability of establishment is conditional on successful germination.

4.4.2 Species specific seed fates under "natural conditions"

In reality, seeds do not receive protection from structures that exclude mammalian predators. Therefore, the un-caged/buried and un-caged/surface treatments were examined for each species per habitat to elucidate the role of scatterhoarders in seed/seedling success (Figures 4.7.1−5). The general effect of caging and burying decreasing the probability of mammalian removal is made evident when considering each species in isolation.

For *A. noldeae*, mammalian removal reduced from >70% in the U/S treatment to <60% in the U/B treatment in all habitats. Despite the higher rates of various seedling mortality factors for the U/B treatment, establishment probabilities for U/B > U/S, but these were reasonably low regardless of habitat (<20%). *A. noldeae* appeared to establish more readily in the EDG and FRG.

Carapa oreophila was the only species where burial did little to prevent seed removal; regardless of habitat or treatment, mammalian removal probabilities were always >80%. As such, the main limiting factor to *C. oreophila* establishment in my plots was mammalian seed predators, and seedling mortality factors had minimal contribution to seed fate. Establishment probabilities were of *C. oreophila* low across habitats and treatments (<10%).

Garcinia smeathmanii exhibited its greatest mammalian removal probability in the EDG. Interestingly, while U/S seeds were most likely to establish in the FRG, U/B seeds were more likely to establish in the COR. While seedling pathogens and mammalian herbivores in the EDG and EDG/FRG (respectively) appear to contribute significantly to mortality, in the COR seed pathogens/desiccation appear to be a greater source of seed death.

Mammalian removal rates for *P. altissima* were high (>50%) in every habitat for U/S seeds, but this was reduced dramatically in the COR/EDG by burial (<20%). The effect of burial was weaker in the FRG, and seed still exhibited high rates of removal (>60%). Seedlings were more likely to establish in the COR, and despite the greater probability of seedling mortality factors in the U/B treatment, burial increased the success of establishment.

Finally, *S. guineense* represents an interesting case in that the probability of mammalian removal was largely lower than all other species (in all habitats) for seeds on the surface. The effect of burial on protecting seeds from mammals was less dramatic in this species, and removal probabilities for *S. guineense* in the U/B treatment were comparable to other species in the same treatment. What is most striking about the fates of *S. guineense* seed is the importance of seedling pathogens and insect herbivory to mortality, which ultimately ended in very low recruitment rates (<10%) in every habitat and both treatments.

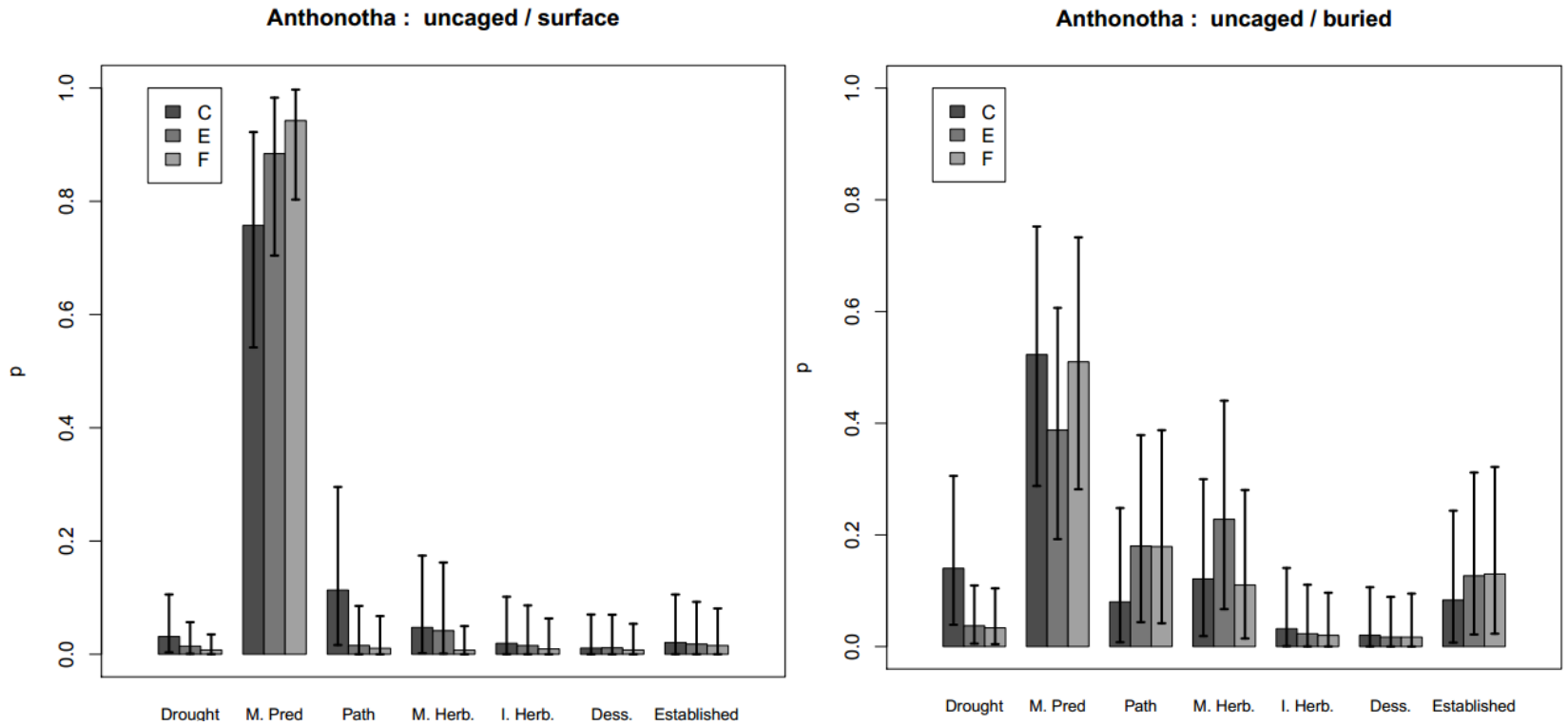

Figure 4.7.1: Seed fates probabilities (with 95% CI) for *A. noldeae* seeds under two simulated natural conditions in the three habitats COR (C), EDG (E) and FRG (F): (left) uncaged and on the surface, and (right) uncaged and buried.

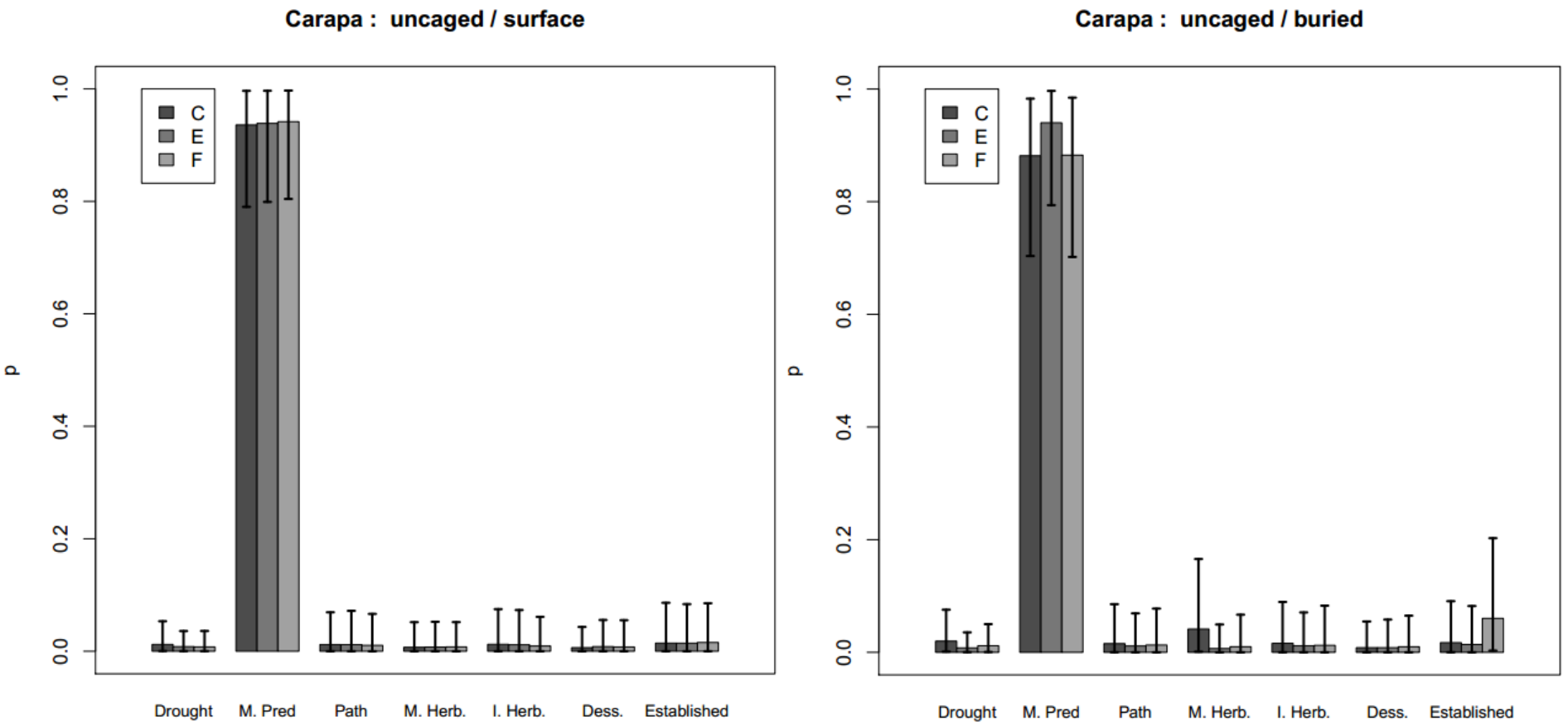

Figure 4.7.2: Seed fates probabilities (with 95% CI) for *C. oreophila* seeds under two simulated natural conditions: (left) uncaged and on the surface, and (right) uncaged and buried.

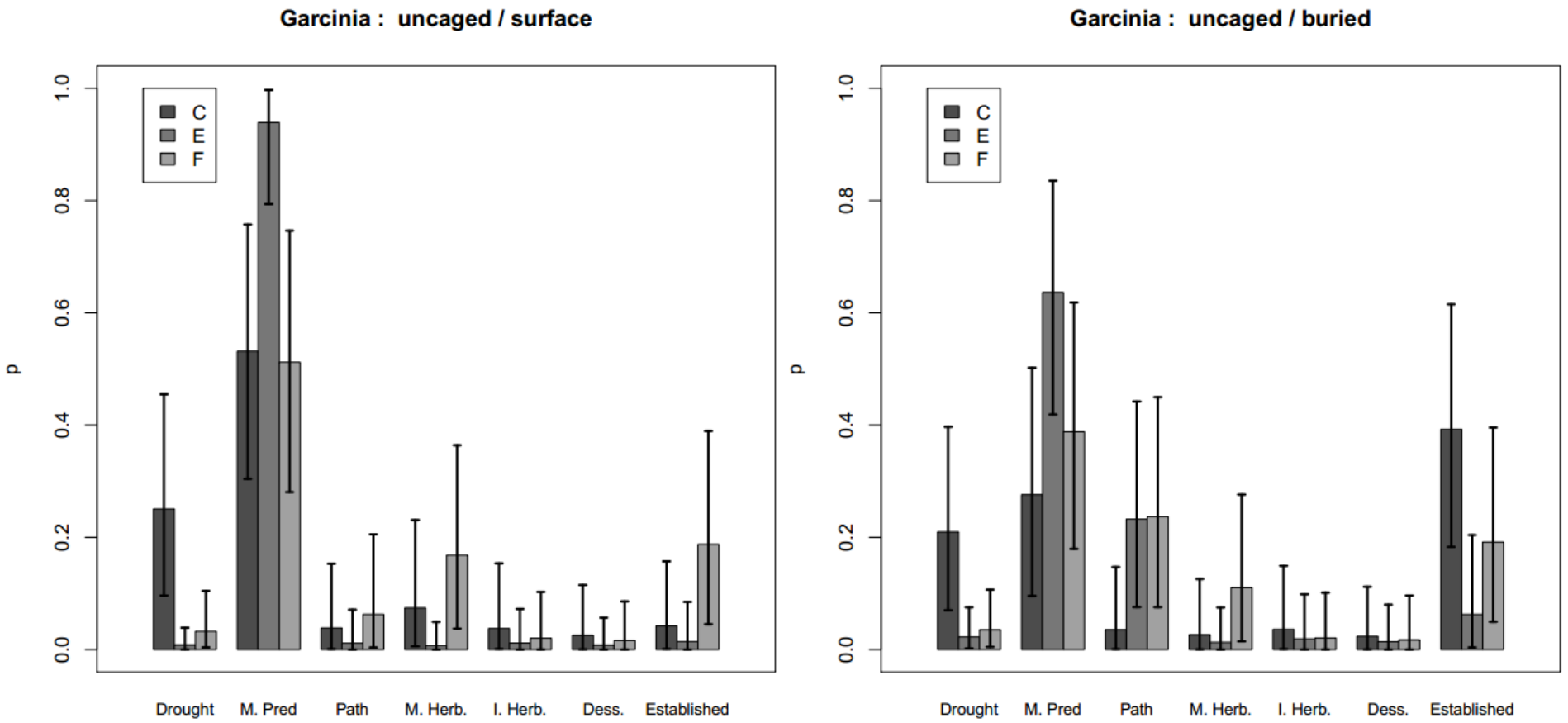

Figure 4.7.3: Seed fates probabilities (with 95% CI) for *G. smeathmanii* seeds under two simulated natural conditions: (left) uncaged and on the surface, and (right) uncaged and buried.

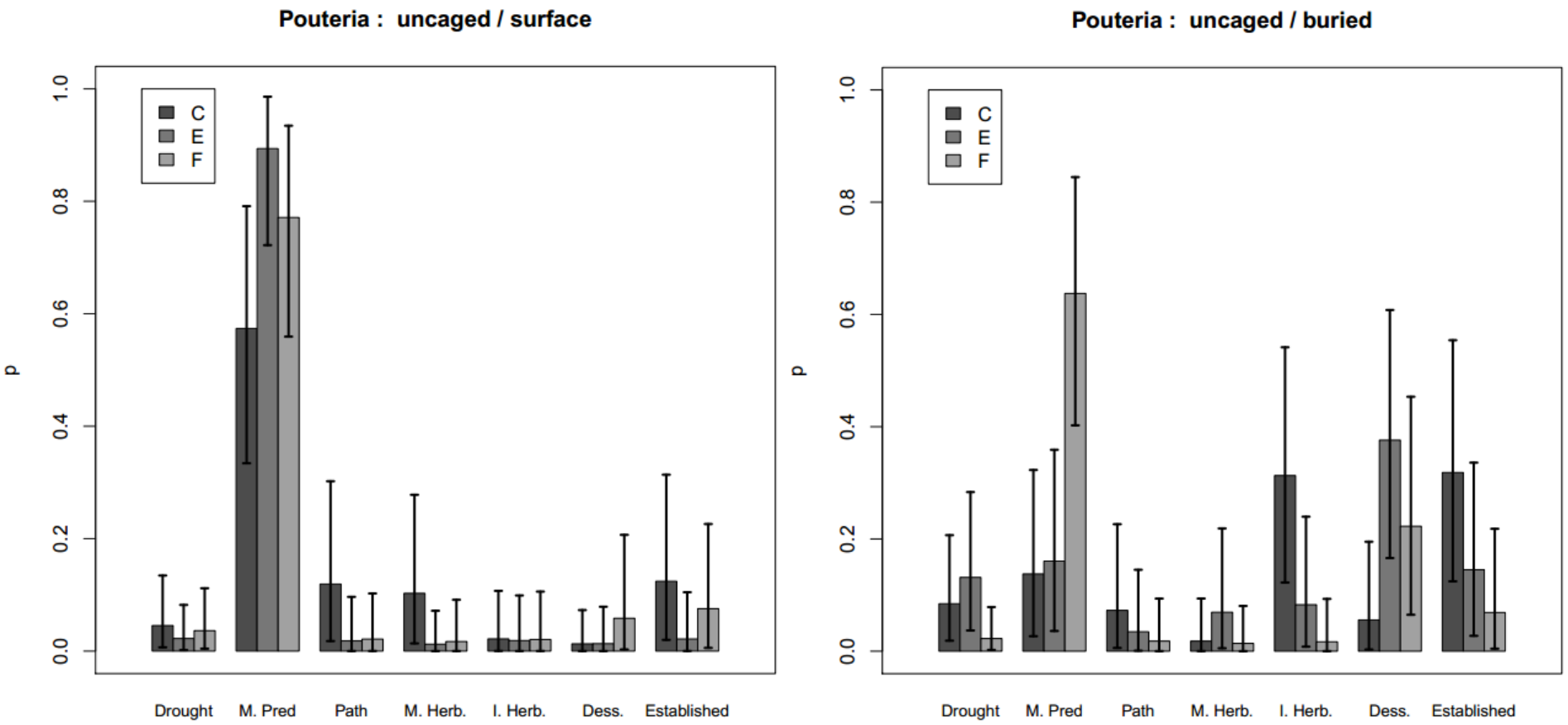

Figure 4.7.4: Seed fates probabilities (with 95% CI) for *P. altissima* seeds under two simulated natural conditions: (left) uncaged and on the surface, and (right) uncaged and buried.

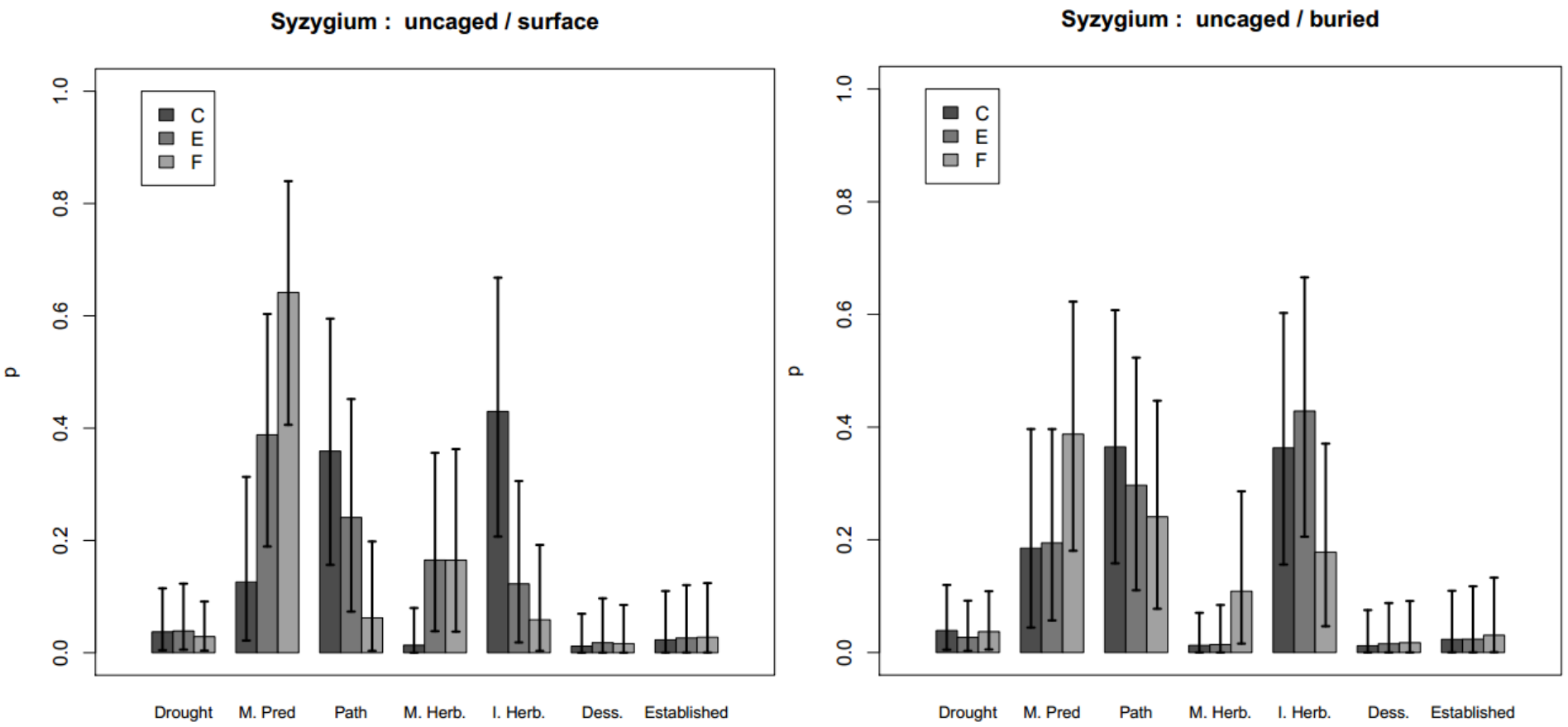

Figure 4.7.5: Seed fates (with 95% CI) probabilities for *S. guineense* seeds under two simulated natural conditions: (left) uncaged and on the surface, and (right) uncaged and buried.

4.5 DISCUSSION

4.5.1 Seed mortality

Predation of seeds on the forest floor can be significantly high (Forget *et al.* 1999; Hall 2008), and exclusion of predators has been demonstrated to positively affect the survival of seeds deposited in the forest (Hall 2008; Hautier *et al.* 2010). Rodent exclusion may have significant consequences for seed viability, such that seed species without rodent protection may exhibit more constrained limits to establishment (Velho *et al.* 2009). While rotting and fungal attack was a source of mortality to seeds, it paled in comparison to seed removal, which was the most significant factor that limited seed survival in the study plots. This was generally consistent across species and factor combinations (habitat, deposition and exclusion treatments), except for *S. guineense*, in which establishment was largely impacted by insect seedling herbivory and attack on seedling by pathogens.

Studies in the tropics (Velho *et al.* 2009; Aliyu *et al.* 2014) and in temperate forests (Myster & Pickett 1993; Perea *et al.* 2011) demonstrate that rodents exhibit preferences, which impacts the removal rates of different seed species. Amongst the five study species, removal probability generally decreased in order of *C. oreophila* > *A. noldeae*>*G. smeathmanii*>*P. altissima*>*S. guineense*. Seeds of *C. oreophila* are large and nutrient rich, which would account for its dramatically greater rates of removal (Vander Wall 2010). It is likely, given the bitter latex in its seed that *S. guineense* might be the least palatable, explaining its much lower probability of removal relative to the other species. It is interesting to note that in this present study, probability of removal for *G. smeathmanii* was greater than *P. altissima*. In a previous study in which these two species were studied together (in isolation from the other three) *P. altissima*was more attractive to rodents than *G. smeathmanii* (Aliyu *et al.* 2014). This could possibly be an artefact of this study: given the large variety of seed taxa available to rodents in the study plot, it could be by chance the difference in preference between *G. smeathmanii* and *P. altissima* was blurred.

In this study, significant positive effects were noted of caging seeds from mammalian removal on seed survival and establishment. In general, these two fates were inversely linked to each other: caged plots had greater establishment of seedlings, whilst uncaged plots had greater removal probabilities and this lead to reduced recruitment in the plot. However, it should be noted that removal from the plot does not necessarily equate to guaranteed mortality. Seeds picked up by rodents may in fact be scatterhoarded considerable distances from their original site of deposition, and some portion of these handled seeds may survive

(Jansen *et al.* 2012a). Dispersal by scatterhoarding rodents has been shown to be advantageous to seeds, including the movement of seeds to discrete sites (burial) where seed predation is low, temperature is maintained and germination is enhanced (Everham *et al.* 1996). However, it has been shown that the decision of rodents to either consume a seed immediately or hide it away for later consumption may be influenced by the ecological context (Theimer 2005; Jorge & Howe 2009; Aliyu *et al.* 2014).

Both Jorge and Howe (2009) and Aliyu *et al.* (2014) in their Neotropical and Afrotropical studies (respectively) demonstrated how habitat plays an important factor in driving scatterhoarding rodent's behaviour. Their results suggested that generally speaking rodents are more likely to hoard seeds in less ecologically degraded habitats (like the interior of the forest), and more likely to consume them immediately in highly degraded habitats (like small forest fragments). This outcome was also influenced by the availability of resources in the focal forests at the time of the experiments. Moreover, Pinto *et al.* (2009) observed higher rates of seed removal and predation in edge habitat versus forest interior for 10 large-seeded tree taxa. Their work suggested that habitat use in concert with the feeding behaviour and demographic patterns of rodents interact to create ecological filters for tree species recruitment.

Under the "natural" conditions treatment (un-caged and seeds deposited on the surface), in accord with other work at Ngel Nyaki Forest (Aliyu *et al.* 2014), this study, I found that habitat largely influenced the probability of mammalian seed removal. These patterns were not straight forward, however, and dependent on the seed species in question. *A. noldeae* and *S. guineense* showed a predictable stepwise pattern of removal probability: COR < EDG < FRG, in which removal increased along the habitat ecological degradation gradient. *G. Smeathmanii* (COR ≈ FRG < EDG) and *P. altissima* (COR < FRG < EDG) removal probabilities were unusual, in which both species exhibited greatest removal in the EDG. *Carapa oreophila* was distinct in that regardless of habitat, all seeds had an extremely high probability of removal (>80%). Studies of other African trees have demonstrated that seed predation need not necessarily increase in fragments, and may in fact be greater in the forest interior: e.g. *Leptonychia usambarensis* (Cordeiro *et al.* 2009).

Finally, I wished to explore how scatterhoarding by rodents might facilitate recruitment. This was done by burying seeds beneath the soil in the experimental plots. Though it has been suggested that the large seeds may have limited escape from predators through burial (Hulme & Teresa 1999), over all species and habitats, the general trend was for

decreased mammalian removal when seeds were buried. Results suggest that buried seeds avoid detection more readily than do their counterparts on the surface. On the one hand, while a seed must be handled by a rodent in order to get buried, burial by one rodent possibly reduces the seed's ability to be detected by other rodents—a benefit which comes at the potential cost of being eaten later.

Another source of seed predation that was not explored directly in this study (but should be addressed) is that of infestation by insects, which can have negative impacts on germination, growth, and mortality of seeds and resultant seedlings (McKenna & McKenna 2006). Predation by invertebrates on seed has been shown to correlate with habitat and plant life form, and different types of invertebrate seed predators may be associated with nutritional characteristics of a seed species (Ramírez & Traveset 2010). It is also highly probable that seeds buried by rodents will escape infestation by insects, given that burial of seeds (incorporated into primate faeces) by dung beetles is correlated to greater escape from rodent predation and increased establishment success of seedlings (Culot *et al.* 2011; Beaune *et al.* 2012).

4.5.2 Seedling mortality

Sources of mortality to seedlings differed amongst species. Across all treatments and habitats, every seed that germinated and produced a seedling had a very low probability of experiencing mammalian herbivory, regardless of taxa. In contrast, insect herbivory was a very significant source of mortality for *S. guineense* seedlings and a reasonable death contributor to *A. noldeae* and *P. altissima* seedlings. In regard to infection by pathogens, *A. noldeae* and *G. smeathmanii* experienced higher probability of attack relative to *C. oreophila* and *P. altissima*, and *S. guineense* had a higher probability of infection with respect to all other species. Finally, between the species, *P. altissima* was most likely to be infected by desiccation.

Seed predation rate was important in fragmented habitat. Like seed mortality, seedling mortality factors are also habitat and species-dependent (Augspurger 1984; Schupp 1988; Benítez-Malvido & Lemus-Albor 2005; Sugiyama & Peterson 2013). Fitness tradeoffs exist amongst species under different microhabitat conditions, and this may be a contributing factor to the coexistence of diverse tree species in the tropics (Baraloto *et al.* 2005). Seedling survival acts as a critical link between dispersal and successful establishment, and whilst a site may be beneficial for a seed, it needs to possess the qualities satisfactory for the resultant

seedling to recruit (Rey & Alcantara 2000).

Bagchi *et al.* (2014) demonstrate that protecting seedlings with insecticide resulted in boosted recruitment due to suppression of insect herbivores. Pathogens can cause significant mortality to seedlings (Augspurger 1984; Bell *et al.* 2006). Water stress can also be a major limiting factor for seedlings (Rey & Alcantara 2000; Engelbrecht *et al.* 2005). Also, exclusion of large vertebrateherbivores has been demonstrated to enhance recruitment of tropical tree seedlings (Terborgh & Wright 1994). The relevance of different mortality factors can be augmented by habitat. Fragment size and edge effects may work synergistically against seedling survival (Benítez-Malvido & Martínez-Ramos 2003), and Benítez-Malvido and Lemus-Albor (2005) demonstrate that pathogen attack on seedlings in edge habitats was three times greater than that in interior forest. While neighbourhood effects (*i.e.* the relative densities of hetero- and conspecific seedlings) can also play a role in seedling mortality (Queenborough *et al.* 2007), but this was likely negligible due to the equal abundance of each seedling species in plots.

4.5.3 Seed germination and establishment

Factors limiting establishment may be life-stage dependent, and those acting on earlier life-stages may represent the major obstacles to successful recruitment (Rey & Alcantara 2000; Sugiyama & Peterson 2013). Species with different ecological strategies will require different microhabitat variables for successful recruitment (Clark *et al.* 1993), and the timing of germination itself is a strategy based on the fruiting phenology and the season at which germination success is greatest (Garwood 1983). The germination of seeds in fragment habitat has been suggested to be less successful than in continuous forest due to a greater precedence of limiting factors (Bruna 1999). This was largely consistent with my study: all species exhibited greater germination in the COR forest relative to the FRG, except for *G. smeathmanii*, in which FRG > COR > EDG.

With respect to the EDG, all species exhibited lower germination at the EDG relative to the COR, except *A. noldeae* (with a germination probability of EDG > COR > FRG). Thus, aside from *G. smeathmanii* and *A. noldeae*, the remaining species (*C. oreophila, P. altissima,* and *S. guineense*) exhibited sequential patterns of germination success probabilities from COR to EDG to FRG. Biotic sources of damage may be exacerbated in edge forest habitat (Benítez-Malvido & Lemus-Albor 2005), and a forest's edge structure is important in determining the dynamics of edge effects—i.e. forests with more open edges will have more

adverse conditions than those with closed edges (Didham & Lawton 1999; Gascon *et al.* 2000). This is important in the context of Ngel Nyaki Forest because the EDG can be highly disturbed: cattle intrude the forest and fire encroaches on its border. As a consequence, much of the ground layer of vegetation in highly disturbed parts of Ngel Nyaki is quite altered, and the herbaceous-shrub zone that buffers the forest/grassland border is, in many places, absent.

Conditions for establishment are probably more stringent than those for germination (Turnbull *et al.* 2000), and the distributions of establishment probabilities (given initial germination) are varied amongst my focal species and habitats. For *G. smeathmanii*, establishment follows the same trend as germination probabilities (FRG > COR > EDG), and the same is roughly true for *A. noldeae* (EDG > COR ≈ FRG). For *P. altissima*—which shows a stepwise pattern for germination probabilities—establishment exhibits a different pattern of COR > FRG > EDG. Finally, *C. oreophila* and *S. guineense* exhibit a reciprocal trend, in which establishment decreases from FRG > EDG > COR. It should also be mentioned that while *S. guineense* exhibited extremely high germination probabilities in all habitats, ultimate establishment probabilities across habitats was always <10%. Of even greater interest is the apparent fact that overall, establishment of seedlings (generalised across species and treatments) was greatest in FRG habitat (> COR > EDG), which was contradictory to what would be suspected given the greater degradation in the FRG. Such results highlight the importance of understanding the disparity between seed and juvenile requirements, as factors that are important for seeds may not be beneficial for establishment or eventual recruitment of a tree species in a particular microsite (Rey & Alcantara 2000) .

The results of this study also demonstrated that overall probability of germinating or establishing is greatest when a seed is buried 50 times and when protected from mammalian predators (caged), with increases (relative to other treatments) of approximately 94 times. For every species, this is largely attributed to the reduction in mammalian removal: seeds buried beneath the surface must obviously be harder to detect, and cages exclude contact of rodents and seeds. Rodents have been demonstrated to exert high predation forces on seeds, which may impact recruitment rates (Hall 2008; Velho *et al.* 2009; Hautier *et al.* 2010); however, at the same time there is at least a potential benefit of being handled by a rodent secondary disperser, as this could lead to burial. Seed traits that affect the choice of rodents to hoard and reduce their detection once they are hoarded should be under selection (Vander Wall 2010).

This study, therefore, suggests that a more efficient alternative to natural regeneration and enrichment planting may be the dispersal of seed by scatterhoarding rodents at suitable

sites over the targeted area. Seeds can easily be collected annually for most African tree species in the region, including *A. noldeae, C. oreophila, G. smeathmannii* and *P. altissima*. Further research on these species' reproduction, seed biology, and demography in post-logged forests is needed to fully evaluate such an approach. More broadly, if dispersal limitation is indeed of primary importance in structuring tropical tree communities, then secondary seed dispersal by rodents may generally offer an effective tool for improving sustainability and mitigating anthropogenic impacts in this diverse ecological system.

4.5.4 Implications for forest management

Despite very different distributions of adult trees and their juveniles across the different forest habitats at Ngel Nyaki, all species (except perhaps *S. guineense* that had exceptionally low rates of two year survival) were able to establish in each habitat. Thus, local distribution, abundance, and regeneration of these tree species could be limited by their ability to disperse (Tilman 1994; Hurtt & Pacala 1995; Hubbell 2011). Meta-analysis by Turnbull *et al.* (2000) suggested that a significant proportion of plants may be seed limited, which is the condition by which population size could be increased if seeds were added. Their review proposed that seed limitation tends to occur more commonly in early successional habitats and early successional species. Furthermore, they concluded that, given many studies observed ability for successful establishment in sites where the species was previously absent, immigration of propagules could enhance local diversity.

All the focal seed species in this study are reasonably large, requiring animal dispersal. Cordeiro and Howe (2001) found that non-animal dispersed trees appear to recruit just as well in small fragments as in large forests; however, animal dispersed species recruited poorly with decreasing fragment size, as indicated by declining densities of smaller size classes in fragments. Large-seeded tree species may therefore be more susceptible to fragmentation, because their major dispersers are restricted to areas of greater forest cover (Cramer *et al.* 2007b).

However, dispersal of the study species is most definitely not the only explanation for the highly divergent frequencies of adults and juveniles observed between species and habitat types (Aliyu unpubl. data). This is evident from the differences in: (1) interspecific germination and establishment rates; and (2) the intraspecific establishment rates per habitat and the associated intensity of different mortality drivers to seeds and seedlings that act as filters to recruitment. The ability for large-seeded species to disperse into sites, and

subsequent post-dispersal limitation factors on seedling survival interacts to determine the abundance and distribution of tropical tree recruits (Dalling *et al.* 1998; Dalling *et al.* 2002). In the case for *S. guineense*, while seed removal was a significant limiting factor, there was a much greater precedence of seedling mortality factors that drastically drove down its establishment. In contrast, the major cause of establishment failure in the remaining focal species was removal by rodents.

Ultimately, the processes identified here will have community consequences in regard to species composition and the ability for the forest to regenerate. It has been proposed that reforestation in Neotropic forests are largely limited by constrained seed dispersal and/or competition of tree seedlings with pasture grasses (Holl *et al.* 2000; Wijdeven & Kuzee 2000). Ideally, restoration efforts in a fragmented forest system (like that at the Ngel Nyaki Reserve) need to work on countering forces that further degrade forest fragments, increasing the diversity of species that are attractive to vertebrate seed dispersers, and ultimately extend the area of forest cover and coalesce fragments (Janzen 1988). While eliminating the anthropogenically-driven degradation of Ngel Nyaki will prove difficult, based on the results of this study, assisted regeneration and expansion of the main and riparian forests can be made. Most obviously, artificial sowing of seeds is likely to prove less effective—given the relatively high rates of rodent removal. Instead, given that germinated seedlings may have reasonable survival, efforts should be made to cultivate seedlings *ex situ* and plant them into the forest.

4.5.5 Conclusions

Our understanding of the effects of fragmentation on ecosystems is still in its infancy- the consequences are not always consistent or predictable. For example, removal of seeds from experimental plots may either increase or decrease in fragments when compared to nearby continuous forest. A lack of top-down regulation on tropical forests has allowed seed predator populations to increase to a degree that seed is being destroyed (Terborgh *et al.* 2001). This is not to claim that other possibilities, such as pollination, seed dispersal, seed germination, or seedling establishment have no role in the process of forest decline. Each possibility should be tested. From the position of where we stand today, excessive seed predation and herbivory appears to be the primary force leading to restoration collapse in fragmented habitats at Ngel Nyaki Forest.

CHAPTER 5

The consequences of habitat degradation on the regeneration processes of selectedtree species.

5.1 DISCUSSION AND SUMMARY

Afromontane forests are one of the most threatened ecosystems in Africa because they are located in areas long favored by human occupation (Hamilton & Perrott 1981) and where human population growth rates are high. The fauna and flora of the Cameroonian Highland forests have high levels of endemism and are a global conservation priority (Fishpool 1997), yet they are poorly protected and highly fragmented. Fragmentation and degradation of West African montane forests is being exacerbated by rapid rates of land clearance for farming and grazing, and where they survive these forests are losing their larger animals (Maisels & Forboseh 1999; Maisels *et al.* 2001; Chapman *et al.* 2004). Loss of frugivores will affect seed dispersal while other factors associated with forest fragmentation and degradation such as fruit abundance (Lopez & Terborgh 2007) and rodent density (Cordeiro & Howe 2003) may shift the balance in seed-rodent interactions from being predominantly mutualistic to predominantlyantagonistic (Jorge & Howe 2009). In addition, other components filtering establishment may change with habitat; herbivory may increase or decrease with fragmentation as may pathogens (Augspurger 1984) and changed abiotic conditions such as increased light and less humidity associated with fragmentation may in some species be detrimental to establishment (Naoe *et al.* (2011). The influence of any one of these factors on establishment will depend on the interplay between the factor and the plant species concerned. Seed size and/or palatability, for example, may influence the probability of a seed being predated vs dispersed.

The aim of this thesis has been to explore the influence of land use change (increasing fragmentation and degradation) on establishment of key montane forest forest tree species in Ngel Nyaki forest reserve, Nigeria.

In Chapters 2 and 3 the interplay between habitat, seed traits (size and palatability) and rodents on seed fate was explored. In Chapter 2 two main hypotheses were tested: firstly that rodents will shift from acting as mutualists in COR forest to predators in fragmented forest and secondly, that this shift will be more extreme in palatable than non palatable seed

species. In Chapter 3 the possibility that rodents are successfully dispersing a tree species which has totally lost its primary disperser was investigated; *Carapa oreophila* has large seeds which have presumably evolved for dispersal by mega-fauna such as elephants but now depend entirely on rodents for dispersal away from the parent tree. Finally, in Chapter 4, using a multifactorial split plot experiment, selective filters that may limit regeneration of the focal trees in the different habitats (COR, EDG and FRG) in Ngel Nyaki Forest Reserve were examined.

5.1.1 The interplay of seeds and rodents

The main findings from Chapters 2 and 3 are that in Nigerian montane forests a single species of rodent, *Cricetomys*sp., commonly referred to as the African pouched rat, scatterhoards large seeds. Relatively high levels of hoarding were recorded; after 10 days at least 60% of *P. altissima* and *G. smeathmannii* (Fig. 2.1b) and 40% of *C. oreophila*(Fig. 3.3) were hoarded (cahed/buried)in the COR.These proportions are comparable with results from some Neotropical studies (Forget 1991, 1994). However, the comparison ends there because in this study the fate of hoarded seeds was not followed systematically; some of the buried seeds did germinate and a very few were dug up and re-cached, but the study did not quantify this. Future investigations should follow the fate of hoarded seeds. The use of radio telemetry of seeds (see Jansen et al. 2012b) would help answer some of these questions. The evidence presented in Chapter 1 (Fig.1.4) of almost no *C. oreophila* seedlings in the forest, strongly suggest that most hoarded *C. oreophila* seeds/seedlings die at some stage.

As with some other studies (Jorge & Howe 2009) the proportion of predated vs hoarded seed increased with fragmentation and forest degradation. However, the trend differed among species. For example in *P. altissima* and *G. smeathmanii*, the effect was greatest at the EDG, where only 43 and 30% respectively were hoarded, compared with ~60% in the COR. In contrast, in the case of *C. oreophila* the effect of fragmentation was greatest in FRG, where only ~15% of seeds were hoarded compared with 40% in the COR. The evidence from the experiments suggested that this difference was mainly due to increased predation rather than anything else and likely reflects both seed availability in the two habitats and rodent densities. In general there was less seed available in the fragments because there are fewer trees with large fruits (Ihuma 2007) but the density of rodents in the different habitats remains unknown. This is another important question that needs answering in future studies. Preliminary investigations into rodent density were attempted but the

density was so high that with the 30 traps available no rats were ever recaptured after marking. Clearly in future studies high trap densities are needed.

Overall the results of chapters 2 and 3 illustrate the fact that large seeded tree species are threatened by fragmentation and 'edge effects' in this montane landscape.

In addition to habitat, seed fate was also influenced by season (Figure 3.4) as regards to*C. oreophila*, and palatability (Chapter 2) as regards to *P. altissima* and *G*. s*meathmanii*. The probability of *C. oreophila* seeds being hoarded was markedly higher in the second season of the fruiting period than any of the other three season blocks. This could present a window of opportunity—seeds scatterhoarded during this period may be sufficiently high in number for regeneration. However, again, almost no seedlings were ever found in the COR, despite this being the habitat into which most seeds were hoarded. Interestingly, more *C. oreophila* seedlings were noted growing in EDG than in the COR (Fig. 1.4) This suggests that perhaps despite high predation rates in the EDG, there is sufficient hoarding for some regeneration and that habitat (light) may be more important for regeneration than predation. Possibly however, for *C. oreophila* predation rates in the FRG are just too high to allow for regeneration.

In summary seed in the FRG and EDG were more likely to be consumed immediately (as opposed to hoarded) and were moved considerably shorter distances relative to the COR. The greater palatability of *P. altissima* exacerbated the effect of forest degradation on antagonistic rodent behaviour. From this, it would seem that more palatable species are likely to experience a greater probability of secondary dispersal failure due to fragmentation and habitat degradation. As a consequence, regeneration patterns may be altered and this could alter community composition in the forest's long-term future.

It was concluded that *Cricetomys* pouched rats in Ngel Nyaki may indeed at least partially fill an important dispersal role that has been left open since the disappearance of mega-fauna in the area (elephants have been locally extinct for at least 60 years). However, their effectiveness will depend on the habitat and the seasonal variance in fruiting, both of which impact resource abundance and the choice of whether or not to hoard or immediately consume seed.

5.1.2 Establishment filters and seed fate

Quantifying the relative importance of the multiple processes that limit seedling establishment may hold the key to understanding tropical tree species diversity (Hurtt & Pacala 1995). Therefore, in chapter 4, an assessment was made of how fragmentation and habitat degradation is likely to shape patterns of seedling establishment of tree species inhabiting Ngel Nyaki. Of the five selected tree species (*C. oreophila*, *A. noldeae*, *G. smeathmannii,P.altissima* and *S. guineense*), while germination rates were reasonably high by and large, seedling establishment and (survival to two years), was considerably lower. Although seeds of all the species germinated in all three habitats, habitat filtering and post-establishment mortality strongly limited seedling establishment.

This thesis demonstrated that in general, the rates of seed germinating versus establishing across the COR, EDG and FRG forests differ widely amongst species. Overall, seeds that are buried and excluded from vertebrate predators observe significantly greater survival odds (>50%; Fig. 4.4); however, the relative importance of various seedling mortality factors (pathogens, vertebrate and invertebrate herbivory) depends on the species and the habitat (Fig. 4.7.1−5). Thus it seems that a combination of seed limitation (i.e. a lack of seed dispersal of particular species into a habitat type) and establishment limitation (i.e. a lack of adequate conditions for a seed/seedling's success) may limit recruitment in a species- and habitat-specific way. Consequently, changes in land use that change the forest's environment could impact regeneration and species distribution patterns in the future.

5.2 Management implications

While montane forests may naturally be fragmented (Eeley *et al.* 1999), human presence in the area has undoubtedly lead to severe habitat degradation (Chapman *et al.* 2004; Adanu *et al.* 2010). Given the fact that seeds of the focal species germinated and established across all habitats, this suggests that restoration is possible and the general abundance and distribution of species can be increased. Because this study demonstrated that larger-seeded species are particularly prone to mammalian predation, it is advised that seeds are grown *ex situ* and planted into the forest.

However, restoration of Ngel Nyaki Forest is likely to face a number of challenges. Successful strategies that will facilitate restoration in fragmented forest must simultaneously overcome cattle grazing around the forest and bush burning. Pearson (2002) indicates that the

efficiency of restoration is influenced by the health and characteristics of the surrounding landscape; for example, increased exposure of fragmented habitat to human impact can reduce restoration capacity. In the immediate future of restoration of Ngel Nyaki Forest, an opportunistic but targeted response by land management such as the Ministry for Environment and the state Land and Survey are possible avenues for establishing reliable restoration management measures.

In terms of future work it is recommended that the seedlings monitored in this experiment for two years continue to be monitored into the future. This will give valuable information on establishment filters post seedling stage. Another future direction could be using the seedlings that are already established in the forest (naturally) and monitoring them. Using naturally established seedlings would allow for larger sampling sizes and may allow for treatments to be imposed such as insecticide, molluscicide and fungicides to farther understand establishment filters.

In the long term, it will be necessary to create appropriate conditions for the participation of all relevant stakeholders in the planning and implementation of restoration initiatives in the Ngel Nyaki Forest. Many hold the view that eliminating poverty is closely linked to forest restoration and conservation of biodiversity particularly in rural areas where people depend on the forest as a means of livelihood.

Future work

Although this study provides data on seed predation, dispersal, distance of dispersed seeds (chapter 2) and subsequent seedling survival to two years, it is only a short term assessment. Growth to reproductive age for large-seeded trees like *C. oreophila*, *A. noldeae* and a palatable medium-seeded *P. altissima* takes decades. In this study, secondary dispersal of seed to long distances (i.e., by scatterhoarding rodents) was a relatively rare event, but this rare event may be important for recruitment. Whether or not *G. smeathmannii* established seedlings in the Ngel Nyaki forest of highest initial survival noted in this study retain that advantage through recruitment to reproductive age awaits data from longer-term studies. Processes such as attack by pathogen, desiccation and herbivory are likely important forlonger-term seedling/sapling survival, especially for large-seeded species.

The next steps could include longer-term studies of recruitment from natural and experimental seed shadows, comparisons of recruitment in species with different fruit and

seed morphologies dispersed by similar dispersers (scatterhoarding rodents), and detailed studies of recruitment for a plant species (or group of related species) at multiple sites. Such studies could lead to fruitful comparative analyses that may address the underlying filters to seedling/sapling survival in the Ngel Nyaki forest.

5.3 CONCLUSION

If Nigeria's montane forests are to survive, and if restoration into degraded areas is to succeed, it is important that we understand how these forests function in terms of plant-animal interactions. The research presented in this thesis pioneers the way to understanding seed fate and filters to establishment in the face of frugivore loss in this montane habitat.

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